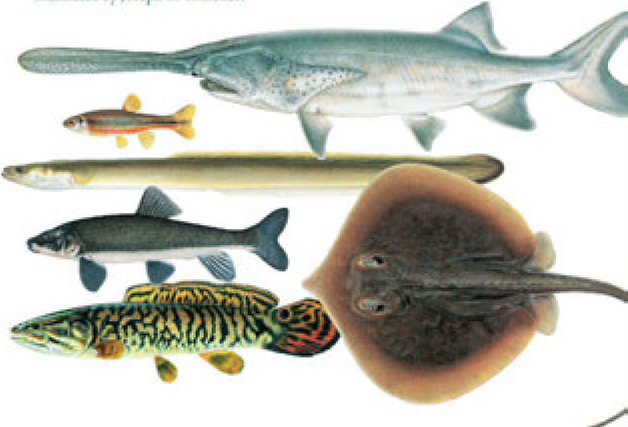
VOLUME 1

Freshwater Fishes of North America

PETROMYZONTIDAE TO CATOSTOMIDAE

Edited by Melvin L. Warren, Jr., and Brooks M. Burr

Illustrated by Joseph R. Tomelleri



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Preface

The North American freshwater fish fauna comprises a little more than 1,200 native species in 50 families. It is the most thoroughly studied and largest temperate fish fauna (Page & Burr 2011) in the world. In comparison, an analysis and compendium of European freshwater fishes included 546 native species in about 24 families (Kottelat & Freyhof 2007); Europe is about one-third the land area of North America. Australia has nearly 300 freshwater fishes in 35 families (Allen 1989; Allen et al. 2002) in a land area about that of the United States (minus Alaska). This number includes many marine species that enter fresh water, and highly unusual freshwater fish lineages occur there (e.g., Salamanderfish, *Lepidogalaxias salamandroides*; Australian Lungfish, *Neoceratodus forsteri*; Nurseryfish, *Kurtus gulliveri*). The only other temperate fish fauna that could rival North America is Asian, but reliable information on this vast area and its fishes remains poorly understood by scientists in the New World. An estimate for the country of China stands at 1,010 native species (M. Kottelat pers. comm.). Unsurprisingly, as for many plant and animal groups, the tropical regions of the world harbor freshwater fish faunas several times larger than those of temperate regions (Lundberg et al. 2000; Berra 2007).

In the mid-1970s knowledge of North American freshwater fishes was confined to a few specialists, but even so for many species (and families) little was available on natural history or ecology. In 1980, a landmark volume was published that used spot distribution maps to illustrate the ranges of all freshwater fish species in the United States and Canada (Lee et al. 1980 et seq.). That volume made available to the lay public as well as specialists a level of knowledge of the North American freshwater fish fauna theretofore unknown. Shortly thereafter a physician from Forsythe, Missouri, combined his hobby of scuba diving and snorkeling with photography and revealed, even to specialists, the incredible colors of the North American native fish fauna, especially in their brightest breeding condition, as well as some of their unique and fascinating natural histories. William N. Roston eventually traveled the continent looking for clear water and fish to photograph in their natural environment (never in aquaria). A number of his photographs are used here.

During this period, numerous books focused on fish faunas of individual states (e.g., Alabama, Arkansas, California, Illinois, Kansas, Mississippi, Missouri, New Mexico, Ohio, Virginia, West Virginia, Tennessee, Washington, Wisconsin) as well as Canada, making even more detail on fishes available to the public. These works allowed for the first complete identification guide to all freshwater fishes in the United States and Canada (Page & Burr 1991, revised 2011). Nevertheless, it was not until the *Freshwater Fishes of Mexico* (Miller et al. 2005) was published that it was possible for us to consider editing this three-volume work on the natural history, ecology, and conservation of North American freshwater fishes. We are indebted to a large community of ichthyologists, fisheries biologists, and other workers in related fields (e.g., physiology, genetics, behavior, ecology) who have investigated the details of the lives of fishes in such a way that much technical information can now be synthesized in one place and again made available to the public and other specialists.

Even though our overarching goal was to synthesize as much information as possible on North American freshwater fishes, the job of gathering information is far from complete. In editing this work and writing synthesis chapters of our own, we were struck at once by the incredible natural history and taxonomic diversity among our native freshwater fishes but also by the large and critical information gaps that remain. Unfortunately, for many species (and nearly entire families), the syntheses presented here are (or are close to being) obituaries. For many species and groups, the biological information needed to help recover them, to slow population declines, or to prevent extinction is simply unavailable. That said, the most critical component of conserving North American freshwater fishes is the prevention of habitat loss and degradation by humans, not lack of biological information. Fishes in this fauna have an incredible tenacity for life, whether we completely understand their biology or not, but we as co-inhabitants of the North American continent need to provide them the opportunity to endure. We hope that this work helps stem the high rates of population decline and extinction being experienced across the North American fish fauna. We also hope this work stimulates a whole new generation of ichthyologists and fisheries researchers to further expand our knowledge and appreciation of the natural history, ecology, and conservation of the great freshwater fish fauna of North America.

AREA AND BREADTH OF COVERAGE

The area of coverage encompasses fishes in fresh waters of North America, including Canada, the coterminous United States, and Mexico, south generally to the Isthmus of Tehuantepec. For some families, authors extended the southern boundary to include fishes of the Yucatan Peninsula region. Within the covered area, all native North American fishes, emphasizing the level of genus, are included that primarily inhabit and reproduce in fresh water and that primarily inhabit marine or estuarine systems but are frequent or even permanent components of some freshwater fish assemblages. Some primarily marine fishes are included because they are naturally established and reproduce in fresh waters (e.g., Atlantic Stingray, *Dasyatis sabina*; Burns et al. this volume). Others are included because young and adults penetrate deeply into freshwater systems and reproduce or are suspected of reproducing in fresh waters (e.g., Hogchoker, *Trinectes maculatus*), and still others simply occur with such high frequency in freshwater habitats that they likely are important functionally in those ecosystems (e.g., Striped Mullet, *Mugil cephalus*). Admittedly, some degree of arbitrariness was unavoidable in the inclusion or exclusion of marine species in a work about freshwater fishes, but the arbitrariness reflects a biologically real gray area among fishes at the interface of saltwater and freshwater systems (e.g., "coastal" Largemouth Bass, *Micropterus salmoides*; Gulf Pipefish, *Syngnathus scovelli*; Atlantic Needlefish, *Strongylura marina*).

Each taxonomic chapter focuses on a family or in some cases two families of North American freshwater fishes with emphasis on the natural history, biology, evolution, and conservation of each genus in the family. The sequence of the families generally follows the arrangement of Nelson et al. (2004) and Nelson (2006). In volume 1, taxonomic chapters cover the Lampreys (Petromyzontidae) through the Suckers (Catostomidae) with one exception. Because of extenuating circumstances, the chapter on Herrings (Clupeidae) will be included in a subsequent volume. Taxonomic chapters in volume 2 will cover the Characins (Characidae) through the Livebearers (Poeciliidae), and volume 3, the Sticklebacks through the American Soles (Achiriidae), but we acknowledge the phylogeny of Ray-finned Fishes and Spiny-rayed Fishes by Near et al. (2012, 2013) and the expansion of that work by Betancur-R. et al. (2013) as the most comprehensive and defensible to date and present those sequences herein for North American fishes we cover (Tables P.1 and P.2).

METHODS

Sources. We encouraged authors to use only peer-reviewed publications in this work, but in many cases information was only available in unpublished dissertations, theses, or even reports. We clearly indicate those unpublished sources as such in the literature cited.

Scientific and common names. For scientific and common names of taxa (e.g., species, genera, families, orders), we used Nelson et al. (2004), Nelson (2006), Page et al. (2013), and occasionally FishBase (2012) as guides. Our order of presentation of families follows that of Nelson (2006), but as noted previously, Near et al. (2012, 2013) presented a phylogeny of Ray-finned Fishes (Actinopterygii) and Spiny-rayed Fishes (Acanthomorpha) based on 9–10 nuclear genes and 579 fish species. Using and expanding the Near et al. (2012, 2013) data, Betancur-R. et al. (2013) analyzed relationships of 1,401 bony fish taxa using 20 nuclear and 1 mitochondrial genes. The results clearly indicate convergence on a well-resolved phylogeny for most fishes. We accept those works as definitive (Tables P.1 and P.2) but did not follow that phylogenetic sequence due to the timing of preparation for this volume. Authors give the

Table P.1. Phylogenetic sequence, clade names, orders, and family names of Ray-finned Fishes (Actinopterygii) and Spiny-rayed Fishes (Acanthopterygii) represented in North American fresh water. The sequence follows the phylogenetic trees recovered from analysis of 9–10 nuclear genes and 579 fish species (modified from Near et al. 2012, 2013). The designation at the ordinal level of incerti ordis indicates the broader relationships of the family were undefined.

Clade name	Order and family (common name)
Actinopterygii	
Actinopteri	
	Acipenseriformes
	Acipenseridae (Sturgeons)
	Polyodontidae (Paddlefishes)
Neopterygii	
Holostei	
	Amiiformes
	Amiidae (Bowfins)
	Lepisosteiformes
	Lepisosteidae (Gars)
Teleostei	
Elopomorpha	
	Anguilliformes
	Anguillidae (Freshwater Eels)
Osteoglossocephala	
Osteoglossomorpha	
	Hiodontiformes
	Hiodontidae (Mooneyes)
Clupeocephala	
Otocephala	
	Clupeiformes
	Clupeidae (Herrings)
	Engraulidae (Anchovies)
Ostariophysi	
Otophysi	
	Cypriniformes
	Catostomidae (Suckers)
	Cyprinidae (Carps and Minnows)
	Characiformes
	Characidae (Characins)
	Siluriformes
	Ariidae (Sea Catfishes)
	Heptapteridae (Seven-finned Catfishes)
	Ictaluridae (North American Catfishes)
Euteleostei	
	Salmoniformes
	Salmonidae (Trouts and Salmons)
	Esociformes
	Esocidae (Pikes and Mudminnows)
	Osmeriformes
	Osmeridae (Smelts)
Neoteleostei	
Eurypterygii	
Ctenosquamata	
Acanthomorpha	
	Percopsiformes
	Amblyopsidae (Cavefishes)
	Aphredoderidae (Pirate Perches)
	Percopsidae (Trout-Perches)
	Gadiformes
	Gadidae (Cods)

(*continued*)

Table P.1., continued

Acanthopterygii				
	Percomorpha			
			Syngnathiformes	
				Syngnathidae (Pipefishes and Seahorses)
			Gobiiformes	
				Gobiidae (Gobies)
				Eleotridae (Sleepers)
			Synbranchiformes	
				Synbranchidae (Swamp Eels)
			Pleuronectiformes	
				Achiridae (American Soles)
				Paralichthyidae (Sand Flounders)
				Pleuronectidae (Righteye Flounders)
		Ovalentaria		
			Atheriniformes	
				Atherinopsidae (New World Silversides)
			Beloniformes	
				Belonidae (Needlefishes)
				Hemiramphidae (Halfbeaks)
			Cyprinodontiformes	
				Rivulidae (New World Rivulines)
				Goodeidae (Goodeids)
				Profundulidae (Middle American Killifishes)
				Cyprinodontidae (Pupfishes)
				Fundulidae (Topminnows)
				Poeciliidae (Livebearers)
			incerti ordinis	
				Cichlidae (Cichlids and Tilapias)
			incerti ordinis	
				Mugilidae (Mullets)
				Embiotocidae (Surfperches)
			incerti ordinis	
				Gobiesocidae (Clingfishes)
		Unnamed clade		
			Centrarchiformes	
				Centrarchidate (Sunfishes)
			Perciformes	
				Percidae (Perches)
				Cottidae (Sculpins)
				Gasterosteidae (Sticklebacks)
		Unnamed clade		
			incerti ordinis	
				Moronidae (Temperate Basses)
		Unnamed clade	incerti ordinis	
				Sciaenidae (Drums)

complete scientific and common name in the chapters on first mention of the species and thereafter use either or both. Authors were free to deviate from these primary sources for common and scientific names for newly described species and higher taxa or because of differing or new systematic evidence (or taxonomic opinion) as well as for clarity. We capitalized the common names, if available, of all species, families, orders, and higher taxonomic categories (e.g., Ray-finned Fishes for Actinopterygii, Eels for Anguilliformes, Freshwater Eels for Anguillidae, American Eel for *Anguilla rostrata*) (see Nelson et al. 2002). We encouraged authors to use the common name in lieu of scientific names after first mention because common names are descriptive and colorful and are increasingly more stable through time than scientific names. We did not capitalize colloquial, nonstandard,

Table P.2. Phylogenetic classification of Ray-finned Fishes (Actinopterygii) represented in North American freshwaters. The sequence follows the phylogenetic tree recovered from analysis of DNA sequence data for 20 nuclear and 1 mitochondrial genes for 1,401 bony fish taxa plus 4 tetrapod species and 2 chondrichthyan outgroups representing 1,093 genera and 369 families (Betancur-R. et al. 2013). The designation at the ordinal level of incerti ordinis indicates the broader relationships of the family are undefined.

Class **Subclass** **Infraclass** **Megacohort**	**Superorder**	**Order**	**Family (Common Name)**
Actinopteri			
Chondrostei		Acipenseriformes	Acipenseridae (Sturgeons)
Neopterygii			Polyodontidae (Paddlefishes)
Holostei		Amiiformes	Amiidae (Bowfins)
		Lepisosteiformes	Lepisosteidae (Gars)
Teleostei			
Elopocephali		Anguilliformes	Anguillidae (Freshwater Eels)
Osteoglossocephalai		Hiodontiformes	Hiodontidae (Mooneyes)
		Clupeiformes	Clupeidae (Herrings)
			Engraulidae (Anchovies)
	Cypriniphysae	Cypriniformes	Catostomidae (Suckers)
			Cyprinidae (Carps and Minnows)
	Cypriniphysae	Characiformes	Characidae (Characins)
	Cypriniphysae	Siluriformes	Ariidae (Sea Catfishes)
			Heptapteridae (Seven-finned Catfishes)
			Ictaluridae (North American Catfishes)
		Salmoniformes	Salmonidae (Trouts and Salmons)
		Esociformes	Esocidae (Pikes)
			Umbridae (Mudminnows)
		Osmeriformes	Osmeridae (Smelts)
		Percopsiformes	Amblyopsidae (Cavefishes)
			Aphredoderidae (Pirate Perches)
			Percopsidae (Trout-Perches)
		Gadiformes	Gadidae (Cods)
			Lotidae (Cuskfishes)
		Gobiiformes	Eleotridae (Sleepers)
			Gobiidae (Gobies)
		Syngnathiformes	Syngnathidae (Pipefishes and Seahorses)
		Synbranchiformes	Synbranchidae (Swamp Eels)
		Pleuronectiformes	Achiridae (American Soles)
			Paralichthyidae (Sand Flounders)
			Pleuronectidae (Righteye Flounders)
		incerti ordinis	Embiotocidae (Surfperches)
	Cichlomorphae	Cichliformes	Cichlidae (Cichlids and Tilapias)
	Atherinomorphae	Atheriniformes	Atherinopsidae (New World Silversides)
	Atherinomorphae	Beloniformes	Belonidae (Needlefishes)
			Hemiramphidae (Halfbeaks)
	Atherinomorphae	Cyprinodontiformes	Cyprinodontidae (Pupfishes)
	Atherinomorphae		Fundulidae (Topminnows)
	Atherinomorphae		Poeciliidae (Livebearers)
	Atherinomorphae		Goodeidae (Goodeids)
	Atherinomorphae		Profundulidae (Middle American Killifishes)
	Mugilomorphae	Mugiliformes	Mugilidae (Mullets)
	Blennimorphae	Blenniformes	Gobiesocidae (Clingfishes)
		incerti ordinis	Moronidae (Temperate Basses)
		incerti ordinis	Sciaendae (Drums)
		Centrarchiformes	Centrarchidae (Sunfishes)
			Elassomatidae (Pygmy Sunfishes)
		Perciformes	Percidae (Perches)
			Gasterosteidae (Sticklebacks)
			Cottidae (Sculpins)

or semi-technical, but informal, common names for groups of fish (e.g., brook lamprey, shad, carp, dace, minnow, pikeminnow, shiner, chub, buffalo, carpsucker, redhorse, jumprock, piranha, bullhead, madtom, salmon, trout, pickerel, splitfin, killifish, molly, mosquitofish, bass, blackbass, crappie, darter).

Fossil taxa. We indicated fossil taxa by a dagger "†" placed before the genus name. In general, we followed Walker & Geissman (2009) for designation of geologic time (period, epoch, age) in millions of years ago (mya), but the original references should be consulted to determine how the geological formations were dated or how fossil dates were estimated.

Abbreviations and museum acronyms. We abbreviated standard length, total length, and fork length as SL, TL, and FL, respectively. Museum acronyms followed Leviton et al. (1985) and Leviton & Gibbs (1988).

Distributional maps. We provided to authors shaded maps for each genus showing the estimated native freshwater range of the genus in North America. For genera with expansive marine ranges, the freshwater and nearshore marine range is given, not the entire marine range. Although we took care to make the maps as accurate as possible, the scale of the maps and shading of the range obviated pin-point accuracy. Also, for many fishes that have been widely introduced, the native range can only be estimated from often limited historical data.

TAXONOMIC CHAPTER ORGANIZATION

With a few exceptions (e.g., Lampreys, Petromyzontidae), each taxonomic chapter contains 13 major sections and various numbers of subsections. For some families, little to nothing may be known about certain sectional and subsectional topics, and in those cases, the paucity or lack of information is generally acknowledged.

Even in a work this large and broad ranging, we came to realize early on that some important topics could not be covered adequately when our focus was largely at the level of genus. Hence, contributors did not cover the zoogeography of species within each family. The zoogeography of North American freshwater fishes would require another volume to update and reassess information previously synthesized on that topic (e.g., Hocutt & Wiley 1986; Mayden 1992; see also Ross & Matthews, this volume). Likewise, contributors did not include tools or aids in identification of species (e.g., illustrated keys) because identification is most often a species-level exercise and it is so well covered in numerous state and regional fish books, including Canada (Scott & Crossman 1973) and Mexico (Miller et al. 2005; see also literature guide sections in each taxonomic chapter), as well as in a field guide for North American freshwater fishes north of Mexico (Page & Burr 2011). Another important, but large topic not covered in detail is the area of fishing statistics, which again is deserving of a separate synthesis (but see commercial importance sections). We describe the content of major sections and subsections in each chapter as follows.

Chapter introduction. In an initial section, authors introduce the family to the reader by relating the scientific and common names of the fishes, highlighting some specialized or unusual features of the group, and for those families with a large number of marine species or those not wholly endemic to fresh waters of North America, placing the focal taxa in context of the diversity and geographic distribution of the entire family.

Diversity and distribution. Contributors summarize the general diversity of the focal family, including a discussion of each genus, its native distribution, the number of species in each genus, and evidence of polytypy or phylogeographic structure. Authors also included a non-native distribution subsection if information was available outlining introductions outside the native range and, if known, the effects of the taxa as non-natives.

Phylogenetic relationships. Contributors cover all phylogenetic hypotheses (those based on cladistic methodologies) for the focal family (inter- and intrafamilial) identifying, if possible, the sister group of the family and then detailing the relationships of all genera within the family.

Fossil record. Authors summarize the fossil history, if any, for the focal family. Minimally the section synthesizes information on each known fossil genus in the family and the number of extinct fossil species in each genus. Ages or approximate ages are given when known.

Morphology. Contributors synthesize information on morphological structures with an emphasis on diversity in morphology across family members and specialized, unusual, and unique features. In the introductory subsection, authors describe the general physiognomy of the respective family (e.g., body shape; fin shape, type, relative size, and placement; mouth size and placement; scale type, color, and pigmentation patterns). In other subsections, authors detail unusual or specialized external and internal anatomical characteristics (e.g., reproductive anatomy, sensory organs, functional biology, and ecomorphology).

Genetics. Contributors synthesize genetic-based studies focusing on topics such as karyology, phylogeography, infraspecific variation, and hybridization and introgression. They also present studies employing genes or gene products to determine phylogeny in the phylogenetic relationships section.

Physiology. Authors highlight the incredible diversity of physiological traits exemplified by fishes in each family. When information is available, the sections include syntheses on tolerances to and effects of water temperature, dissolved oxygen, pH, salinity, and turbidity. Contributors also highlight other specialized physiological adaptations of each family (e.g., swimming performance, sensory physiology, chemical ecology, bioenergetics, metabolism).

Behavior. Contributors cover non-reproductive-associated behaviors in this section. These include behavioral areas such as aggression, dominance, learning, memory, migratory and non-migratory movement, diel activity, schooling behavior, foraging behavior, alarm signaling, patch choice, and any other unique or specialized behavior.

Reproduction. Authors synthesize features of the reproductive cycle, including reproductive behaviors. The section focuses on topics such as age and size at maturity; sexual dimorphism; spawning migrations, cues, and sites; pre-spawning and spawning behaviors; male and female reproductive allocation; parental care; unusual mating systems; and embryo and larval development.

Ecology. Minimally contributors focus on habitat, diet (particularly diet breadth and specializations), predation, and parasitism but also when possible range across topics from autecology to the functional importance of individual taxa in communities and ecosystems.

Conservation. Authors discuss imperiled fishes in the focal family and the likely reasons for their decline. Contributors incorporate the best available information and summarize the reasons for declines or anticipated declines.

Commercial importance. Contributors cover economic importance and values of taxa in the focal family. This includes the importance in historic or present commercial fisheries, cultural significance, aquaculture, sport fisheries, and the aquarium trade.

Literature guide. In the final section, authors point the reader to major sources of information on the family. In particular, detailed family, species, or topic-specific treatments are referenced.

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COLOR PLATES AND PHOTOGRAPHS

We used color drawings by Joe Tomelleri, the premier fish artist in North America, to illustrate as many North American genera as possible. The colors are as seen on the fishes when they are first removed from the water, and many were drawn when at their peak breeding colors. Joe's fish portraits are done in Berol Prismacolor pencils, and using those pencils Joe is renowned for precisely portraying life color, scale and fin-ray counts, and a full spread of the fins. We express our appreciation to Joe for granting us a generous licensing arrangement for use of his drawings.

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Uland Thomas; Michael Tobler; C. Vaughn; G. Verrault; and Tim Watts, glooskapandthefrog.org/eel%20gallery.htm. Likewise, we gratefully acknowledge Noel M. Burkhead, Stephen T. Ross, and William N. Roston for granting us and the contributors blanket permission to use any of their fish photographs.

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Freshwater Fishes of North America

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Chapter 1

Evolution and Ecology of North American Freshwater Fish Assemblages

Stephen T. Ross and William J. Matthews

Fish assemblages in North America comprise a rich array of species with attendant diversity in morphology, physiology, behavior, ecology, life history, and range of habitats. We suspect that, among the world's largest continental fish assemblages, the North American assemblage has the distinction of being the most thoroughly studied. Even so, much remains to be learned at even the most basic levels. Indeed, anyone who has written, or read, a regional fish book should be impressed immediately by how little is known about most species, especially in regard to the availability of information across the species' ranges. Our goal in this chapter is to synthesize information concerning aspects of the evolution and ecology of fish assemblages in North America. To keep this effort manageable, we have focused on what we believe are some key biological elements of patterns and responses. The unifying theme is to provide an understanding of what controls the kinds and numbers of species in a local fish assemblage. We include information on general origins of North American fishes, ages of assemblages, distributions, and the responses of assemblages and species to habitat characteristics (size, quality, diversity, and variation), resource acquisition, and species interactions. Following Matthews (1998), we consider a fish assemblage to include fish species found together in a single locality over a short ecological time period, i.e., those that have a reasonable probability of encountering each other within the course of feeding, resting, movements, and so forth in a given day.

Fish Diversity

Fishes make up more than half of all extant vertebrates with 27,977 named species and an average of 200 new species described annually (Eschmeyer 1998; Nelson 2006). Of the world's fish fauna, Cohen (1970) estimated that 41.2% were essentially restricted to fresh water. This number is remarkably close to the current number of 43%, or 11,952, recognized freshwater species worldwide (Nelson 2006). This diversity is particularly surprising given that liquid fresh water only makes up 0.0142% of the water on our planet (Shiklomanov 1993). The bulk of the world's fresh water is unavailable as fish habitat because it is frozen (78%) or is groundwater (22%) (Horn 1972; Goldman & Horne 1983).

Considering the six major zoogeographic realms (reviewed by Berra 2007), the greatest freshwater fish diversity occurs in the Neotropical realm (Central and South America and tropical Mexico) with an estimated 5,000–8,000 species, followed by the Oriental realm (India and Southeast Asia) with about 3,000 species, the Ethiopian realm (Africa and southern Arabia) with about 2,850 species, the Nearctic realm (North America except tropical Mexico) with 1,061 species, the Palearctic realm (Europe and Asia north of the Himalayas) with 552 species, and the Australian realm with 500 species, including marine fishes that enter fresh water (Burr & Mayden 1992; Matthews 1998; Lundberg et al. 2000; Moyle & Cech 2004; Berra 2007). These numbers sum to more than that given in the preceding paragraph because some regions include estimates of as yet undescribed taxa, for instance, the most recent estimate raises the number of North American freshwater fish species to 1,116 (Smith et al. 2010). The North American species are included in 201 genera and 50 families, including various marine, peripheral species (Burr & Mayden 1992).

North American freshwater fish diversity is greatest in the southeastern region of the United States, which contains more than half (560 described species) of the freshwater fish fauna (Warren et al. 2000). Western North American fish diversity is about one-third that of overall eastern diversity, although endemism tends to be greater in the west (Moyle & Herbold 1987; Burr & Mayden 1992). In the United States and southern Canada, geographic grids of 1 degree latitude and longitude contained on average ≤10 species in western areas with maximum values of 19 in Oregon, 14 in California, and 11 along the Colorado River (McAllister et al. 1986). In contrast, the same-sized grids in the southeastern United States supported ≤73 species. Another treatment of North American diversity patterns including Mexico further illustrates this pattern (G. R. Smith in Lundberg et al. 2000; Smith et al. 2010; Fig. 1.1).

Regional differences in native fish species can be appreciated more readily by comparing the native species diversity that normal sampling effort (0.75–1.0 h of seining) might yield along several hundred meters of stream. This also relates more closely to the actual richness of fish assemblages. In species-rich southeastern streams, as in Mississippi or in the Ozark Plateau, capture of 25–35 species from a medium-sized stream is not unusual (STR & WJM pers. obs.), compared with 8–12 species in central Oklahoma (Matthews 1998), or <10 species in western North America (Moyle & Herbold 1987). Even so, numbers can vary widely depending on local stream size or environmental conditions.

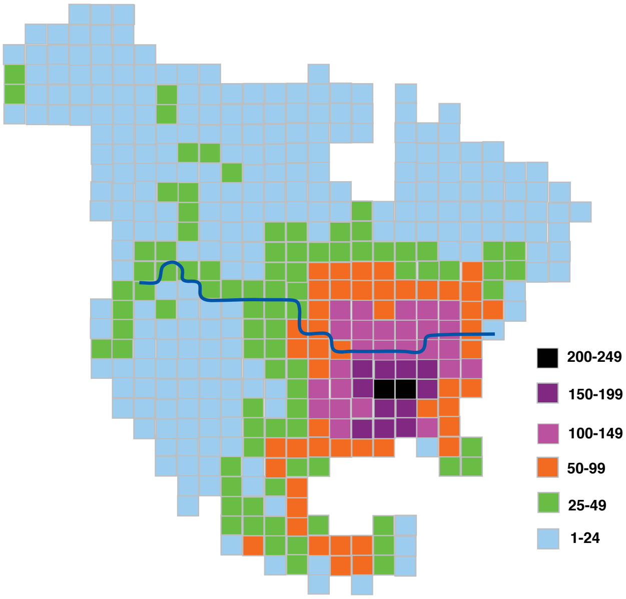

Figure 1.1. Geography of fish diversity in North America and the limit of Pleistocene glaciation (solid blue line). Key shows number of species/grid (reproduced with permission from G. R. Smith).

Habitat

Worldwide, the amount of fresh water is greater in lakes, which, considering only freshwater habitats, have almost two orders of magnitude more volume (98.88%) than streams (1.12%) (Shiklomanov 1993). Human activities have further increased the amount of lentic habitat through the impoundment of rivers. Worldwide >45,000 dams with a height ≥15 m are capable of storing about 15% of the world's annual river runoff (Nilsson et al. 2005). Of the 74 large North American rivers with a virgin mean annual discharge of >350 m^3/s, 39 were judged to be moderately to strongly affected by impoundments or flow regulation (Dynesius & Nilsson 1994). Of the 35 rivers judged not affected, only one, the Pascagoula River, Mississippi and Alabama, is located south of Alaska or Canada.

The preponderance of lentic (lakes, ponds, artificial impoundments) versus lotic (flowing water) habitats might suggest that lake fishes would dominate the diversity of freshwater fishes in North America, and at least in some regions of the world, lake fish assemblages are diverse and may support a high degree of endemism (e.g., Fryer & Iles 1972; Echelle & Kornfield 1984; Smith & Todd 1984). In present-day North America, however, the number of species unique to lakes is much lower than those in flowing waters, primarily because of the young age of large North American lakes (G. R. Smith 1981). New World Silversides (Atherinopsidae: *Menidia* spp.) from Mexico's largest natural lake, Lake Chapala on the Mexican Plateau, provide an example of a small North American species flock with 12 species either restricted to the lake or also occurring in the surrounding streams (Barbour 1973; Miller et al. 2005). The Laurentian Great Lakes also support (or supported because three taxa are now extinct) perhaps nine species of ciscoes (family Salmonidae, Trouts and Salmons, subfamily Coregoninae) (Underhill 1986; Cudmore-Vokey & Crossman 2000; Etnier & Skelton 2003). These are considered an incipient species flock (Smith & Todd 1984). The known native fish fauna of the Laurentian Great Lakes, excluding the St. Lawrence River and tributaries and including extirpated or extinct taxa, comprises 126 species (Cudmore-Vokey & Crossman 2000; Etnier & Skelton 2003), but only 5% are endemic (primarily ciscoes, *Coregonus* spp.) (see Cudmore-Vokey & Crossman 2000). The Great Lakes fauna is derived primarily from the upper Mississippi River drainage, streams of the Atlantic Coastal Plain, and the Beringian Refugium of the Yukon Valley following retreat of the Pleistocene glaciers (Underhill 1986; Mandrak & Crossman 1992). In contrast, 17.9% of the rich lotic Tennessee River fish fauna (about 229 species and subspecies) is endemic (Etnier & Starnes 1993; Warren et al. 2000).

Although North American lakes presently do not support large species flocks, this has not always been the case. Examples of now extinct North American lacustrine species flocks include the fossil Sculpin fauna (Cottidae, genera *Myoxocephalus* and *Kerocottus*) of the Pliocene (5.3–2.6 mya) Glenns Ferry Formation, Idaho (G. R. Smith 1981), and the rich, extinct semionotid fauna from the Mesozoic (251–65.5 mya) Newark lakes of eastern North America (McCune et al. 1984).

Recognizing the influence that species from lotic environments have on lentic assemblages, Kitchell et al. (1977) proposed the term "River Analogy" to explain the distribution of large percid fishes (e.g., Walleye, *Sander vitreus*). They argued that most North American and European lakes were of recent origin (i.e., Pleistocene or later, ≤2.6 mya), that lake-inhabiting fishes had a riverine ancestry, and that pool habitats in low-gradient rivers (sloughs, oxbows) were analogous to littoral lake habitats. We suggest, like Kitchell et al. (1977), that the River Analogy applies to many other groups of lake-inhabiting fishes in North America. Further, fishes of large rivers may use habitats in new lakes (or impoundments) similarly to use of their unimpounded, large-volume habitats (e.g., Blue Catfish, *Ictalurus furcatus*, versus Channel Catfish, *I. punctatus*, in Lake Texoma, Edds et al. 2002). Thus, it is often useful to divide North American fishes on the basis of lentic and lotic habitats especially at a more local scale. On a broader scale, however, this may not be the most meaningful ecological axis along which to consider fish assemblages. We suggest that an equally meaningful axis would be upland versus lowland forms.

ORIGIN AND AGE OF NORTH AMERICAN FISH FAMILIES

Fishes constituting a given assemblage often are considered to have similar origins and histories of interactions; however, this may not be true (Brooks & McLennan 1991; Matthews 1998). Contemporary species assemblages may be due to the association of the species' ancestors in that particular geographic region, or the species may have evolved among different assemblages and entered the assemblage through dispersal. For example, many fishes occurring in Arkansas have affinities with faunas to the north or northeast, but many others are more associated with faunas of the southeastern or southwestern United States. Within one watershed (Piney Creek), 43 fish species had affinities with faunas to the northeast, east, and southeast (Matthews 1998). Because of this, any assemblage is likely a mixture of species that have different origins and evolutionary ages and have been interacting for widely different periods of time. This situation is now made even more extreme by the widespread and relatively rapid introduction of non-native species (Courtenay et al. 1986; Fuller et al. 1999; Gido & Brown 1999; Gido et al. 2004) and the resulting homogenization of faunas (Rahel 2000, 2002, 2010). The mass invasion resulting from the bypassing of natural barriers that have existed in many instances since the Early or Middle Triassic (235–250 mya) represents a new and unique form of global change (Olden 2006; Ricciardi 2007).

A conceptual model for natural colonization of a habitat is that of a series of filters that block potential species at various levels (Fig. 1.2; Smith & Powell 1971; Tonn et al. 1990; Poff 1997; Matthews 1998; Jackson et al. 2001; Rahel 2002). Here, we use this model as the framework for understanding the factors affecting the composition of local fish assemblages. In terms of understanding the origin of specific assemblages, one must also consider the history of lineages leading to particular species, and because of the continuing role of natural selection in conjunction with environmental change, the role of speciation and extinction in affecting the structure of a specific assemblage (see branching lineages, Fig. 1.2).

Teleosts likely arose in the Middle or Late Triassic (202–234 mya) of the Early Mesozoic, and based on the fossil record, representative forms of half of the extant 40 teleostean orders were present at least by the Cretaceous of the Late Mesozoic, some 68–145 mya (Nelson 2006; Helfman et al. 2009; geologic times from Walker & Geissman 2009). Earlier, beginning in the Late Paleozoic (about 306 mya), precursors to present-day continents formed a single large, dynamic land mass, Pangaea, which persisted through the Triassic (202–251 mya) before separating by the Middle Jurassic (about 161–176 mya), forming major northern (Laurasia) and southern (Gondwana) land masses. Proto–North America included western Laurasia. Continued rifting resulted in the gradual breakup of Laurasia and Gondwana into the present-day arrangement of continents (Cracraft 1974; Briggs 1987;

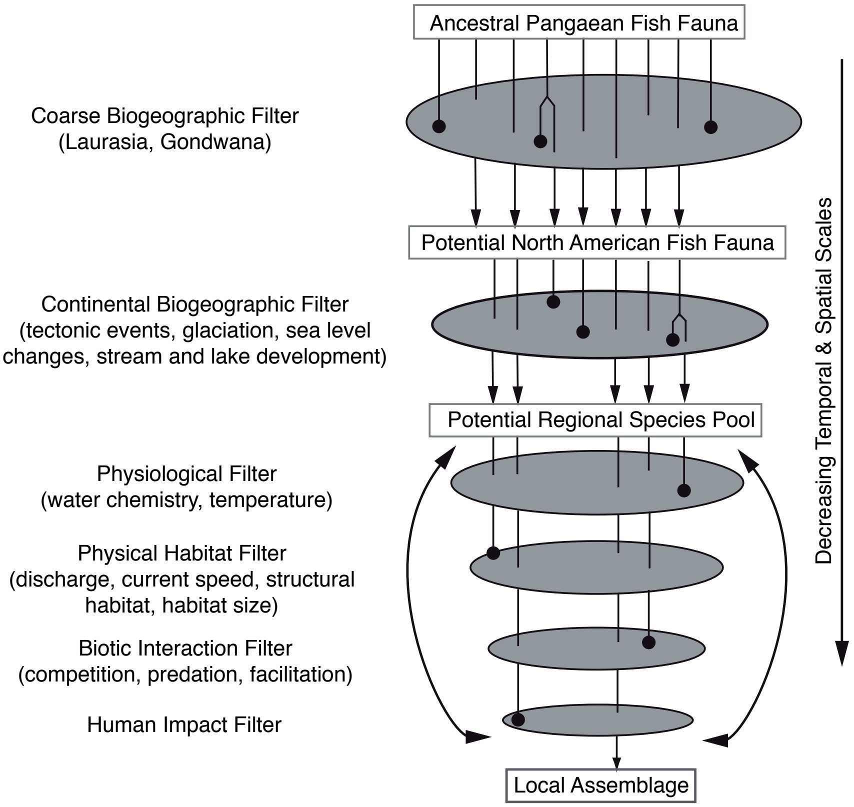
Ancestral Pangaean Fish Fauna
Coarse Biogeographic Filter
(Laurasia, Gondwana)
Potential North American Fish Fauna
Continental Biogeographic Filter
(tectonic events, glaciation, sea level changes, stream and lake development)
Potential Regional Species Pool
Physiological Filter
(water chemistry, temperature)
Physical Habitat Filter
(discharge, current speed, structural habitat, habitat size)
Biotic Interaction Filter
(competition, predation, facilitation)
Human Impact Filter
Local Assemblage
Decreasing Temporal & Spatial Scales

Figure 1.2. A conceptual model of the formation of fish assemblages through progressive loss (i.e., filtration) and addition (i.e., speciation) of lineages. The curved arrows on either side of the figure suggest the interplay between local and regional faunas (adapted in part from Smith & Powell 1971; Tonn et al. 1990; Poff 1997; Matthews 1998; Rahel 2002; Ross 2013).

Hocutt 1987). Because species ancestral to most modern lineages were present before the breakup of Pangaea, the subsequent movements of tectonic plates and their associated faunas were primary factors shaping fish assemblage composition (Fig. 1.2), although in some cases phylogenies are understood too poorly or no fossil material is available to clearly establish an area of origin.

Faunal Origins

North American fish families exhibit a variety of origins, including archaic groups that originated in Pangaea (Fig. 1.3). Of 50 North American fish families (Burr & Mayden 1992), half are of marine origin. In some of these groups, the radiation into fresh water occurred early, such as the Bowfins (Amiidae) in which one subfamily (Amiinae) has occupied freshwater habitats in the Northern Hemisphere since the Late Cretaceous (about 90 mya) (Grande & Bemis 1999). The second largest group has a North American origin and includes lineages originating in Pangaea or Laurasia, followed in number by groups originating in Central and South America and Eurasia (Fig. 1.3).

Although the North American freshwater fish fauna includes at least 50 families, only about half could be considered as major components based on their number of species and/or their breadth of distribution. In addition, 90% of the extant North American freshwater fish species are contained in only 15 families. These families had their origins in Eurasia (Minnows and Carps, Cyprinidae; Suckers, Catostomidae), Central America (Livebearers, Poeciliidae; Topminnows, Fundulidae), North America including Pangean-Laurasian elements (North American Catfishes, Ictaluridae; Trouts and Salmons; Goodeids, Goodeidae; Sunfishes, Centrarchidae; Perches, Percidae), the marine environment (New World Silversides; Pupfishes, Cyprinodontidae; Sculpins; Lampreys, Petromyzontidae; Herrings, Clupeidae), and South America (Cichlids, Cichlidae).

Faunal Ages

The time of occupation of North America by major fish families also varies. Of 27 families or subfamilies for which age data are available (from fossils or from phylogenies calibrated by geological events, fossils, or molecular data), Lampreys (Petromyzontidae) are by far the oldest recorded extant family, dating from the Paleozoic (Fig. 1.4). Other old groups, dating from the Cretaceous Period of the Mesozoic, are Sturgeons (Acipenseridae), Bowfins (Amiidae), Gars (Lepisosteidae), Paddlefishes (Polyodonti-

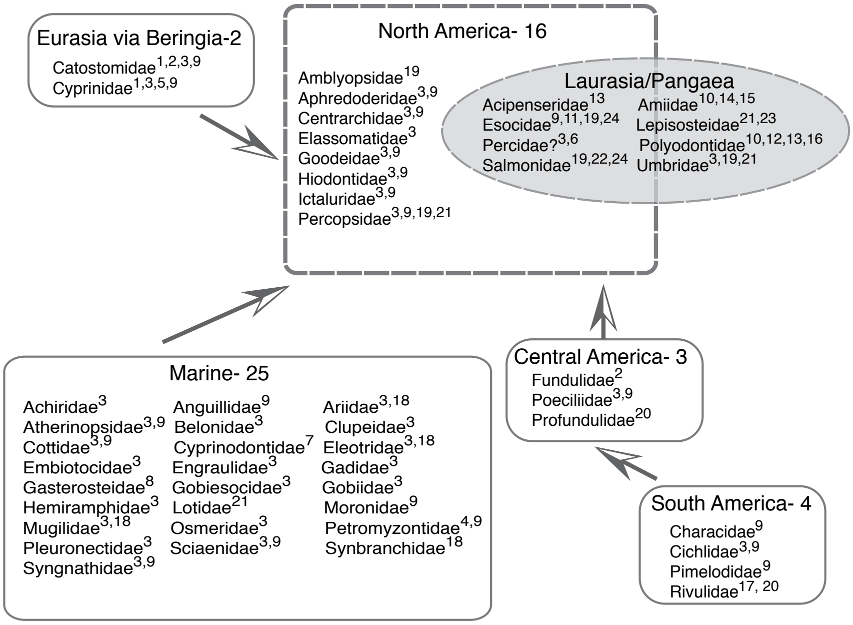
Eurasia via Beringia-2
Catostomidae[1,2,3,9]
Cyprinidae[1,3,5,9]
North America- 16
Amblyopsidae[19]
Aphredoderidae[3,9]
Centrarchidae[3,9]
Elassomatidae[3]
Goodeidae[3,9]
Hiodontidae[3,9]
Ictaluridae[3,9]
Percopsidae[3,9,19,21]
Laurasia/Pangaea
Acipenseridae[13]
Esocidae[9,11,19,24]
Percidae?[3,6]
Salmonidae[19,22,24]
Amiidae[10,14,15]
Lepisosteidae[21,23]
Polyodontidae[10,12,13,16]
Umbridae[3,19,21]
Marine- 25
Achiridae[3]
Atherinopsidae[3,9]
Cottidae[3,9]
Embiotocidae[3]
Gasterosteidae[8]
Hemiramphidae[3]
Mugilidae[3,18]
Pleuronectidae[3]
Syngnathidae[3,9]
Anguillidae[9]
Belonidae[3]
Cyprinodontidae[7]
Engraulidae[3]
Gobiesocidae[3]
Lotidae[21]
Osmeridae[3]
Sciaenidae[3,9]
Ariidae[3,18]
Clupeidae[3]
Eleotridae[3,18]
Gadidae[3]
Gobiidae[3]
Moronidae[9]
Petromyzontidae[4,9]
Synbranchidae[18]
Central America- 3
Fundulidae[2]
Poeciliidae[3,9]
Profundulidae[20]
South America- 4
Characidae[9]
Cichlidae[3,9]
Pimelodidae[9]
Rivulidae[17, 20]

Figure 1.3. General origins of the major families of North American freshwater fishes. Families listed as North American include those of Laurasian-Pangaean origin because of the general uncertainty in determining exact locations. References: (1) Berra (2001), (2) Briggs (1986), (3) Burr & Mayden (1992), (4) Cavender (1986), (5) Cavender (1991), (6) Collette & Banarescu (1977), (7) Echelle & Echelle (1992), (8) Foster et al. (2003), (9) Gilbert (1976), (10) Grande (1984), (11) Grande (1999), (12) Grande & Bemis (1991), (13) Grande & Bemis (1996), (14) Grande & Bemis (1998), (15) Grande & Bemis (1999), (16) Grande et al. (2002), (17) Hrbek & Larson (1999), (18) Miller & Smith (1986), (19) Moyle & Cech (2004), (20) Parenti (1981), (21) Patterson (1981), (22) Smith & Stearly (1989), (23) Wiley (1976), (24) Wilson & Williams (1992).

dae), and Pikes (Esocidae). The remaining North American families all date from within the Cenozoic. Families occupying North America since the Paleogene Period of the Early Tertiary include Ictaluridae, Percopsidae (Trout-Perches), Clupeidae, Salmonidae, Moronidae (Temperate Basses), Hiodontidae (Mooneyes), Catostomidae, Centrarchidae, Aphredoderidae (Pirate Perches), Umbridae (Mudminnows), and Cyprinidae. Families appearing in the Neogene Period of the Late Tertiary include Goodeidae, Poeciliidae, Cichlidae, Percidae, Fundulidae, Cyprinodontidae, Cottidae, Gasterosteidae (Sticklebacks), Atherinopsidae, and Sciaenidae (Drums and Croakers) (Fig. 1.4). Although the earliest percid fossils in North America date only from the Pleistocene, a fossil-calibrated molecular phylogeny of the darters (Percidae, Perches) shows the separation of darters from nondarter percids occurring 19.8 mya (Carlson et al. 2009). Within the darter genus *Nothonotus*, the age of the most recent common ancestor dates to 18.5 mya (Near & Keck 2005). Consequently, percids likely occurred in North America at least by the Early Miocene (about 23 mya). Seventy-eight percent of the 27 major families were present in North America by the Early Miocene (23–16 mya) and were thus affected by numerous geologic and climatic events of the Late Tertiary.

In western North America a freshwater fauna dominated by teleosts first appeared by the Late Paleocene (about 59 mya), followed by the expansion of an essentially modern fauna by the Oligocene and Miocene (Minckley et al. 1986). The western fauna during the Oligocene (23–34 mya) and Eocene (34–56 mya) shared forms with an eastern fauna including Paddlefishes (Polyodontidae), Gars (Lepisosteidae), Sturgeons (Acipenseridae), Bowfins, Trouts and Salmons, Mooneyes, Suckers, North American Catfishes, Trout-Perches, and Pikes (Esocidae) (Grande 1984; Minckley et al. 1986; Grande & Lundberg 1988; Grande 1999). The Oligocene fauna included some of the earlier fauna such as Mooneyes, Trouts and Salmons, Pikes, and also cyprinids, atherinopsids, cyprinodontids, fundulids, gasterosteids, centrarchids, embiotocids (Surfperches), and cottids (Minckley et al. 1986). Of the non-teleosts, Sturgeons are the only extant western forms, but Gars, Paddlefishes, and Bowfins are now absent from the western fauna.

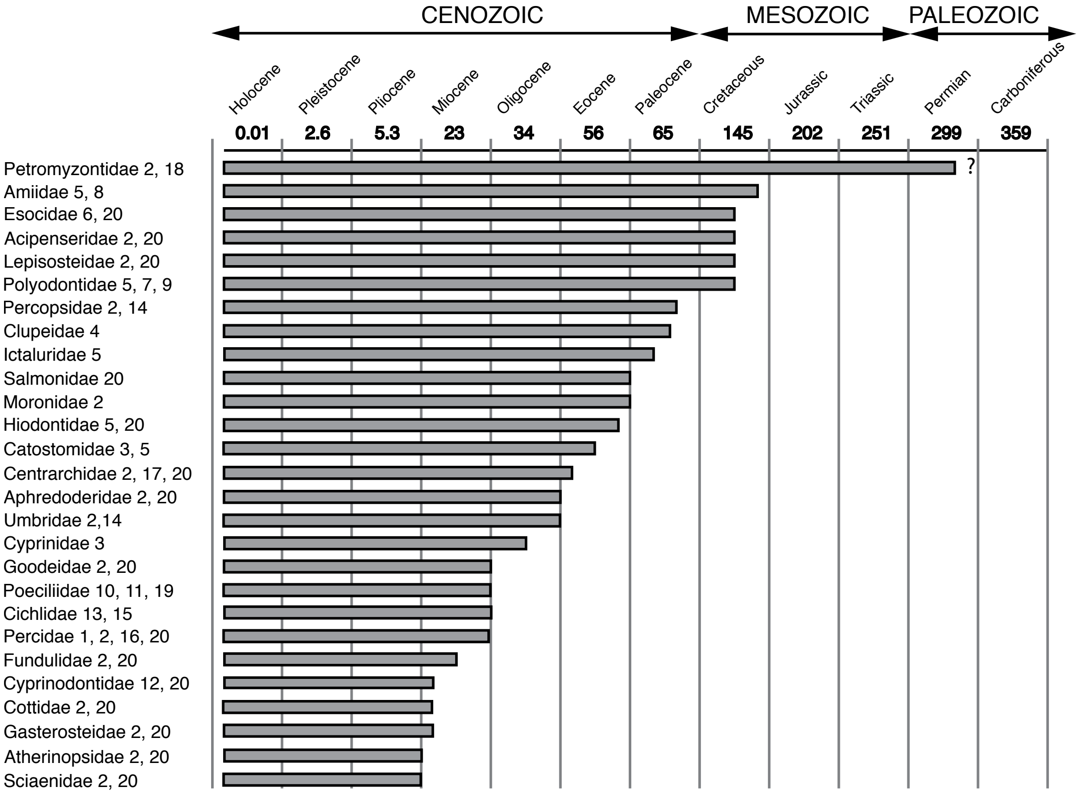

Figure 1.4. The earliest representation of major fish families in North America based on the first occurrence of fossils or from calibrated molecular phylogenies. Because the earliest fossils represent a minimal age of origin, families could be much older. Within the Cenozoic, geologic ages refer to epochs; within the Mesozoic and Paleozoic, ages refer to periods. Numbers at the top of each column are the beginning age (mya) of each geologic age or period. Numbers after families indicate sources; gaps in the fossil record are not shown. References: (1) Carlson et al. (2009), (2) Cavender (1986), (3) Cavender (1991), (4) Grande (1982), (5) Grande (1984), (6) Grande (1999), (7) Grande & Bemis (1991), (8) Grande & Bemis (1996), (9) Grande et al. (2002), (10) Mateos et al. (2002), (11) Meyer & Lydeard (1993), (12) Miller (1981), (13) Murray (2001), (14) Murray & Wilson (1996), (15) Myers (1966), (16) Near & Keck (2005), (17) Near et al. (2005), (18) Nelson (2006), (19) Webb et al. (2004), (20) Wilson & Williams (1992).

The importance of the varying ages of occupation of fish groups in North America to our understanding of fish assemblages is that the forces shaping the evolution of morphology, physiology, and behavior of species making up present-day assemblages are unlikely to be found by looking only within the contemporary assemblage. Instead, selective pressures leading to various traits may date to earlier time periods and may not even include the present-day assemblage. For instance, although feeding and morphological specializations are little changed in Pikes, the community relationships have changed a great deal since the Paleocene (56–66 mya) when Pikes were part of fish assemblages including osteoglossomorphs, percopsiforms, amiids, gonorynchids (Beaked Sandfishes), lepisosteids, asineopids (now extinct), osmerids (Smelts), clupeids, cyprinoids (possibly catostomids), and ictalurids (Wilson & Williams 1992). Thus, major adaptations of Pikes evolved before modern predator-prey systems existed (Wilson & Williams 1992).

Tertiary and Quaternary Events and North American Fish Assemblages

North American fish assemblages were shaped by large-scale geologic and climatic events occurring before and during the Quaternary Period (2.8 mya–present) (Fig. 1.2), and the variation in fish assemblage composition, including species richness along both north-south and east-west gradients in North America, attest to the influence of these intracontinental factors (Fig. 1.1). Middle to Late Tertiary (34–2.6 mya) changes in landform and climate were extensive throughout North America but were particularly so in western North America (Schermer et al. 1984; Dickinson 2004). An extensive geological literature documents that present-day North America west of the Basin and Range Province (essentially comprising the western halves of Washington, Oregon, California, and northern Mexico) and north into Alaska is a conglomerate of allochthonous, accreted terranes of mostly Oceanic origin (reviewed by Minckley et al. 1986). A terrane is a fragment of crustal material formed on, or broken off from, one tectonic plate and accreted to crust lying on another plate. From the Paleozoic through the Late Miocene, these terranes were joined to the North American Craton (= Laurentia) primarily by subduction under the North American Plate (Dickinson 2004). This activity also was directly or indirectly responsible for periods of intense volcanism and orogeny contributing to the formation of the Rocky Mountain Range, the Cascade Range, and later in the Middle to Late Miocene, the Sierra Nevada Range (Schermer et al. 1984; Dickinson 2004; Mulch et al. 2006, 2008; Crowley et al. 2008; Eaton 2008).

Uplift of the Colorado Plateau and formation of the Basin and Range also was related to the subduction of Oceanic plates, in this case the Farallon Plate as it slid beneath the North American Plate (Minckley et al. 1986; Eaton 2008). Although uplift of the Colorado Plateau occurred at least from the Oligocene (about 25 mya), the period of most rapid uplift took place in the Early Pliocene (about 5 mya) (Morgan & Swanberg 1985; Sahagian et al. 2002).

Of importance to our understanding of fish assemblages is that these changes, along with their impacts, extended well into the Cenozoic and were thus recent enough to have affected the flora and fauna of western North America (Minckley et al. 1986). Contiguous patterns of modern fish faunas in the West generally correspond to these continental subplates; drainages that extend across zones into adjacent subplates tend to have faunas derived from several sources (Minckley et al. 1986).

The present-day Colorado River fauna is a case in point. As outlined previously, the regions of the Great Basin and Colorado Plateau (Fig. 1.5) were uplifted primarily during the Early Pliocene (5.3–3.6 mya), and extensive faulting from the Miocene (23–5.3 mya) into the Pliocene resulted in the isolation of the Colorado Plateau when north-trending streams from central Arizona were interrupted. The Early Eocene (56–49 mya) uplift of the Wasatch Front and the subsequent drop of the Great Basin in the Late Oligocene (28–23 mya) isolated the upper Colorado River fauna from that of the Great Basin. The origin of the upper Colorado fauna (including the Green and Colorado River watersheds) occurred before the Miocene in streams draining the uplifted Rocky Mountains and flowing across the Colorado Plateau to interior basins in Arizona, Colorado, and New Mexico (the Miocene Bidahochi

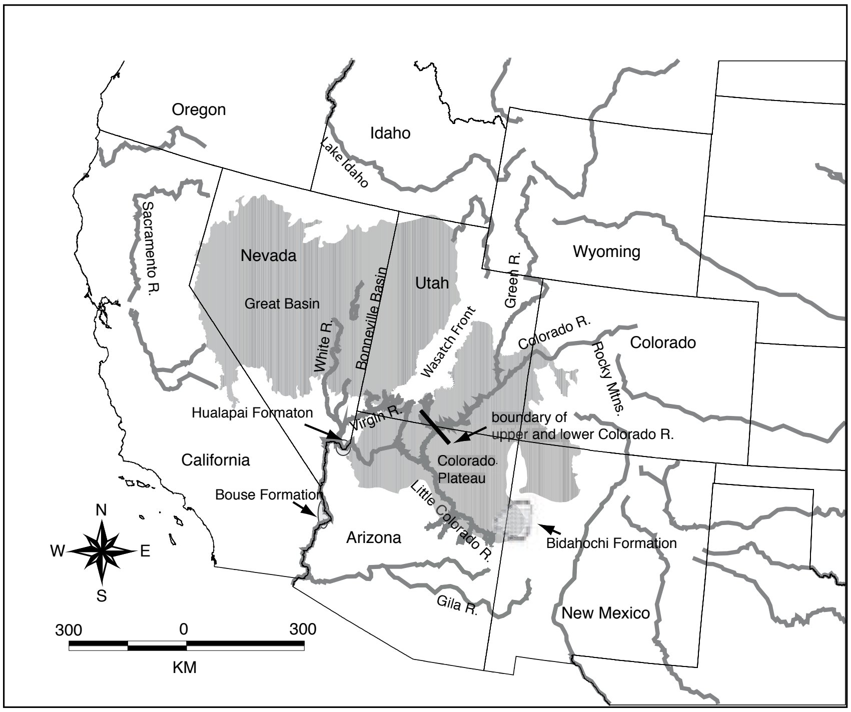
Oregon
Idaho
Lake Idaho
Sacramento R.
Nevada
Great Basin
White R.
Bonneville Basin
Utah
Wasatch Front
Green R.
Wyoming
Colorado R.
Rocky Mtns.
Colorado
Hualapai Formaton
Virgin R.
boundary of upper and lower Colorado R.
California
Colorado Plateau
Bouse Formatio
Little Colorado R.
Arizona
Bidahochi Formation
Gila R.
New Mexico
N
W
E
S
300
0
300
KM

Figure 1.5. The Colorado River drainage and associated geological features (based on Minckley et al. 1986 and Gross et al. 2001).

Basin) or northwestern Arizona (the Miocene Hualapi Basin). A middle section of the Colorado River, currently comprising the Little Colorado, Virgin, and White Rivers, drained to the southwest. A third section, including the Gila River, was incorporated into the drainage after the retreat of the Bouse Miocene–Early Pliocene Embayment (Minckley et al. 1986). The upper and lower Colorado River systems were joined 10.6–3.3 mya via headward erosion of streams of the middle and lower Colorado watersheds and through reoccupation and reversal of flow in older channels. The Colorado River reached the Gulf of California by the Pliocene (Minckley et al. 1986).

Origins of the dominant components of the mainstem Colorado fish assemblage (Colorado Pikeminnow, *Ptychocheilus lucius*; Humpback Chub, *Gila cypha*; Roundtail Chub, *G. robusta*; Bonytail Chub, *G. elegans*; Speckled Dace, *Rhinichthys osculus*; Razorback Sucker, *Xyrauchen texanus*; Bluehead Sucker, *Catostomus discobolus*; and Flannelmouth Sucker, *C. latipinnis*) can be traced to these various geological events (Minckley et al. 1986; Smith et al. 2002c). Species with relationships to the northwest, including the Sacramento–San Joaquin Basin and, more closely, the Bidahochi Lake deposits to the east, include the Colorado Pikeminnow, Roundtail Chub, Humpback Chub, and Bonytail Chub (see also Smith et al. 2002c). The Speckled Dace colonized the upper Colorado River Basin from source populations to the north and west in the northern Bonneville and Snake River drainages about 3.6 mya, and divergence of lineages in the upper and lower Colorado began 1.9–1.7 mya (Oakey et al. 2004; Smith & Dowling 2008). The Flannelmouth Sucker shows relationships to the north and west, but the Bluehead Sucker is related to forms in the Bonneville Basin to the west. Origins of the distinctive Razorback Sucker are less understood, but the divergence of the *Xyrauchen* lineage from that of *Deltistes* and *Chasmistes* likely occurred in the Late Miocene, if not before, and suggests a relationship to the north or northwest (Miller & Smith 1981; Hoetker & Gobalet 1999). Clearly, the main-channel fish assemblage of the Colorado River is a composite of species of different evolutionary origins and ages, and most of the changes predate Pleistocene events.

In addition to geomorphic changes, the composition and distribution of western fish assemblages were shaped by a general climatic trend toward increasing aridity, resulting in the drying of large lakes and shrinking or loss of streams present during the Miocene and Pliocene. In part, the uplift of major mountain ranges contributed to expanding aridity as atmospheric circulation patterns changed and rain shadows formed on the eastern sides of the ranges (e.g., Kohn & Fremd 2008; Mulch et al. 2008). Nowhere is the pattern of increased aridity more striking than in the western Great Basin of what is now Nevada and Utah. During the Early to Middle Pleistocene (about 650,000 years ago), this area, which is now desert, was a land of abundant and large natural lakes, especially Lake Lahontan to the west and Lake Bonneville to the east (Reheis 1999; Mock et al. 2006). As a consequence of overall drying in the region, faunas were increasingly isolated, resulting in high levels of endemism and loss of species through extinction (Hubbs et al. 1974; G. R. Smith et al. 2002). Examples include subspecies and species of desert Pupfishes (*Cyprinodon* spp.) that now exist in isolated spring runs as relicts from once large lacustrine systems, although the divergence times of some lineages or species extend to the Late Pliocene, substantially predating the Holocene desiccation of large lakes (Hubbs et al. 1974; Miller 1981; Smith 1981; Minckley et al. 1986; G. R. Smith et al. 2002; Echelle 2008).

The impact of post-Pleistocene drought on western fishes is further illustrated by work on genetic variability in the Flannelmouth Sucker, one of the ancient, endemic species of the Colorado River (Douglas et al. 2003). Genetic diversity in the Flannelmouth Sucker is surprisingly limited for such an ancient species and is consistent with the hypothesis of a major, basin-wide population crash during a documented post-Pleistocene, severe western drought. Further, populations of this species in the upper Colorado River basin are the result of migration from refugia in the lower part of the system likely within the last 10,000–11,000 years (Douglas et al. 2003; Douglas & Douglas 2010).

Fish assemblages in central and eastern North America also were affected by Late Tertiary (Miocene and Pliocene) (23–2.6 mya) geologic events. One of the most species-rich areas in North America is the Central Highlands region (Fig. 1.6). Various authors have summarized information on Pliocene and Miocene drainage patterns of this area and demonstrated that biogeographic patterns of modern fish assemblages in the Central Highlands are often better explained by these early drainage patterns, especially the Old Mississippi and Teays River systems, than by Pleistocene or Holocene (2.6 mya–present) drainage patterns (Pflieger 1971; Wiley & Mayden 1985; Mayden 1987b, 1988). Abundant biogeographical and geological data support the existence of a Central Highlands province present at least from the Eocene (56 mya) (references in Mayden 1985a, 1987ab, 1988; Wiley &

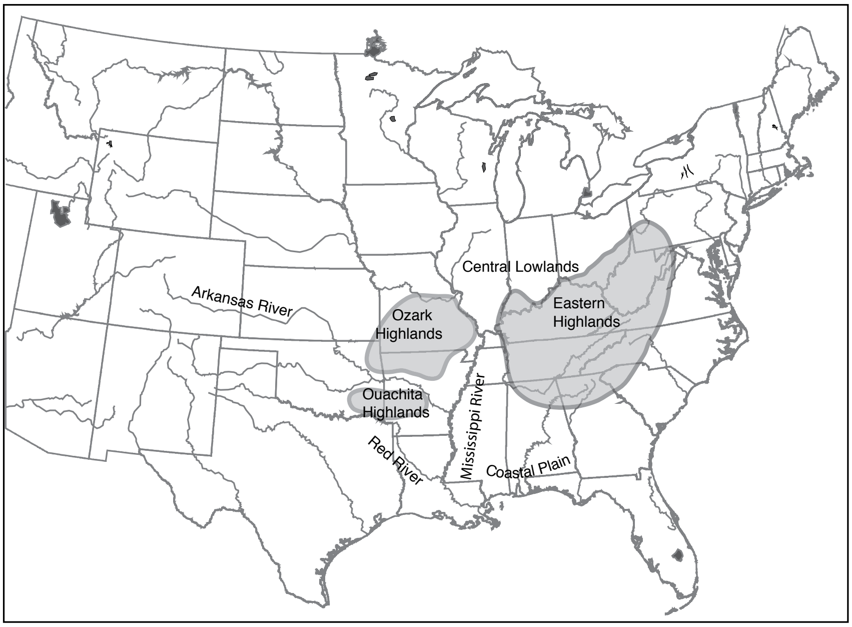

Figure 1.6. The Central Highlands region of eastern North America showing current river drainages (based on Mayden 1987a, 1988).

Mayden 1985). During the Pleistocene, southward movement of pre-Wisconsinan glaciation split the Central Highlands into Eastern and Interior Highlands. This was followed by the penetration of the lowland area connecting the Eastern and Interior Highlands by the Mississippi River, now enlarged because of southward deflection and increased flow of streams that formerly drained into Hudson Bay (Missouri River) or the Laurentian stream system and the Atlantic Ocean (Ohio River) (Pflieger 1971; Mayden 1985a; Wiley & Mayden 1985).

Two principal hypotheses have been proposed to explain the high diversity of the region: the Pleistocene dispersal hypothesis and the Central Highlands vicariance hypothesis (CHVH) (Mayden 1988; Strange & Burr 1997; Near & Keck 2005). In the former hypothesis, the Eastern Highlands represented a center of origin for lineages that subsequently dispersed along glacial fronts during the Pleistocene to streams of the Interior (Ozark and Ouachita) Highlands. As such, species in the Interior Highlands should be no older than the Pleistocene. The CHVH predicts that the fauna diversified in a widespread and interconnected Highlands region during the Miocene and Pliocene and was then fragmented by Pleistocene events, after most speciation events had occurred, into the Ozark and Ouachita Highlands west of the Mississippi River and the Eastern Highlands east of the Mississippi River (Fig. 1.6). Other studies, however, indicate that understanding fish diversity in the Central Highlands is more complex than first thought (Strange & Burr 1997). Phylogeographic analyses using molecular data do show some support for predictions of the CHVH in divergence times of various lineages. The darter subgenera *Litocara* (genus *Etheostoma*) and *Odontopholis* (genus *Percina*) have species in the Ozark and Eastern Highlands and both groups show deep divergences of species between the two regions that likely occurred in the Miocene (Strange & Burr 1997). Four species of the minnow genus *Erimystax*, which occur in the Ozark, Ouachita, and Eastern Highlands and adjoining areas, also show Miocene speciation events (Simons 2004), and divergence within the hogsuckers (genus *Hypentelium*) occurred prior to the Pleistocene (Berendzen et al. 2003). Not all evidence, however, supports Miocene or Pliocene ages of species. In a study of lineage divergences in the 20 species of the darter genus *Nothonotus*, times ranged from the Miocene (6 events) to the Pliocene (4 events) to the Pleistocene (8 events) (Near & Keck 2005). Divergences of subspecies of the Northern Studfish, *Fundulus catenatus*, occurred by dispersal or peripheral isolation in the Late Pleistocene or later; divergence of subspecies of the Banded Sculpin, *Cottus carolinae*, perhaps by peripheral isolation, also occurred in the Pleistocene (Strange & Burr 1997), as did divergence within the Gilt Darter (*Percina evides*) (Near et al. 2001). In summary, the rich Central Highlands ichthyofauna seems to be a product of both vicariant and dispersal events, facilitated by the region's great age and topographic diversity, and the high fish diversity in many ways follows predictions of island biogeography theory and species-area relationships (Page 1983; Near & Keck 2005).

Pleistocene impacts through glaciation, changes in stream patterns caused by ice dams, flow changes, stream captures, sea level lowering, alteration of land by glacial scour, and creation of new lake habitats through terminal moraines or kettle lake formation all had major effects on fish assemblages in northern North America (Pflieger 1971; Crossman & McAllister 1986; McPhail & Lindsey 1986; Matthews 1998). Previously, four major glacial advances were recognized within the Quaternary; however, the estimate of the number of glacial advances from the dawn of the Pleistocene (about 2.6 mya) is now 18–20 for the entire planet and 13–18 for North America (Davis 1983; Ehlers 1996). The last major advance (the Wisconsinan) reached its maximum extent 8,000–10,000 years ago (Ehlers 1996; Lowe & Walker 1997). In addition, there were climatic fluctuations embedded within each of the major advances. For instance, the Wisconsinan glaciation can be subdivided into three periods of advances with the last advance starting about 23,000–25,000 years ago (Ehlers 1996). The limits of glacial advance (Fig. 1.1), defined by terminal moraines or existing waterways, extended the farthest south in the central United States, reaching across Illinois, Indiana (except the south-central region), and most of Ohio nearly to the present course of the Ohio River (Frye et al. 1965; Goldthwait et al. 1965; Wayne & Zumberge 1965; Clark et al. 1996; Lowe & Walker 1997). Farther east, ice covered upper Pennsylvania and all of New York and New England (Muller 1965; Schafer & Hartshorn 1965). Except for montane glaciers, glacial penetration was less in western states, covering the upper half of most of Washington, Idaho, and Montana and all but the southwest corner of North Dakota (Flint 1971). Higher elevations along the Rocky Mountains supported extensive glaciers as far south as New Mexico (Richmond 1965). In the far west, there were large glaciers in the Sierra Nevada Range and even in the transverse ranges of southern California (Owen et al. 2003).

Pleistocene events resulted in substantial changes to earlier drainages so that faunas of present-day rivers may reflect contributions from once separate drainages. For instance, the modern fish fauna of the Red River of the South and its tributaries (Fig. 1.7) likely comprise older faunas from three distinct, pre-Pleistocene river systems: the Plains Stream in the headwaters of the Red River, the Old Ouachita River (Little-Kiamichi-Ouachita system), and the Old (lower) Red River (Mayden 1985a). The amalgamation of faunas is illustrated by examining the biogeographic relationships of 13 fish species taken in a single sample from the Ouachita River, Arkansas (STR pers. obs.; Table 1.1). Five species are endemic, or largely so, to all three regions of the Central Highlands and thus would have had the potential for interaction since the Pliocene

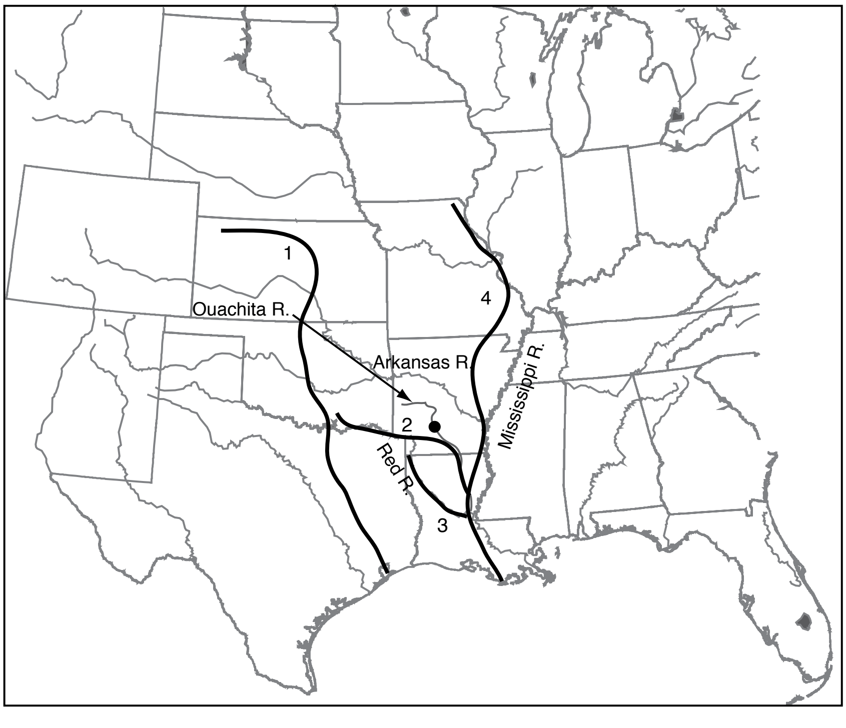

Figure 1.7. The relationship of the modern Red River to pre-Pleistocene drainages. Pre-Pleistocene drainages are shown in black: 1—Plains Stream; 2—Old Ouachita River; 3—Old Red River; 4—Old Mississippi River. Ancestral drainages are based on Mayden (1987a, 1988). The closed circle shows the 1997 collecting site on the modern Ouachita River referred to in Table 1.1.

Table 1.1. Biogeographic relationships of species from a sample of fishes (STR pers. obs.) from the Ouachita River, Arkansas, at the confluence with the Little Missouri River. (1) Found in all Central Highlands (some with disjunct populations in Central Lowlands); (2) endemic to Ouachita Highlands; (2a) Ouachita Highlands and various adjoining regions; (3) widespread, primarily lowland species with sister-species found in Central Highlands (i.e., cladogenesis likely before uplift of Central Highlands); (4) widespread but biogeographically non-informative species.

Taxa	Origin/Pre-Pleistocene Distribution	References
Highland Stoneroller, *Campostoma spadiceum*	2	Mayden (1987a); Blum et al. (2008); Cashner et al. (2010)
Blacktail Shiner, *Cyprinella venusta*	3	Mayden (1987a)
Steelcolor Shiner, *Cyprinella whipplei*	1	Mayden (1987a)
Redfin Shiner, *Lythrurus umbratilis*	4	Mayden (1987a)
Bigeye Shiner, *Notropis boops*	1	Wiley & Mayden (1985); Mayden (1987a)
Bullhead Minnow, *Pimephales vigilax*	4	Mayden (1987a)
Creole Darter, *Etheostoma collettei*	2	Mayden (1985a)
Orangebelly Darter, *Etheostoma radiosum*	2	Page (1983); Mayden (1985a, 1987a)
Speckled Darter, *Etheostoma stigmaeum*	3	Page (1983); Simon (1997)
Redspot Darter, *Etheostoma artesiae*	3	Mayden (1985a); Piller et al. (2001)
Mountain Madtom, *Noturus eleutherus*	1	Mayden (1985a, 1987a)
Banded Darter, *Etheostoma zonale*	1	Page (1983); Mayden (1988)
Channel Darter, *Percina copelandi*	1	Mayden (1987a)

or earlier. Four species are primarily restricted to the Ouachita Highlands and perhaps had a later origin. The remaining five species are widespread, generally lowland forms, some of which are sister species to forms occurring in the Central Highlands. Clearly, even in this example of one sample of fishes, evolutionary origins, ecological histories, and ages of the taxa are different with the assemblage including groups fragmented from a once intact pre-Pleistocene Central Highlands fauna, more recent taxa endemic to the Ouachita Highlands, and components derived from generally widespread, primarily lowland, pre-Pleistocene taxa. Such separate origins have substantial consequences for the interpretation of factors like co-evolution of species' traits (see later treatment herein).

Farther west, in addition to portions of the Missouri River that originally flowed northward into Hudson Bay, the Bonneville Basin was also likely once part of the Hudson Bay drainage during the Late Miocene via the upper Snake River (G. R. Smith 1981; Crossman & McAllister 1986). The connections are reflected in the current fish faunas where, for instance, the Bonneville drainage (located primarily in Utah) contains faunal elements from the north and northeast such as *Prosopium* spp. (whitefishes), *Catostomus* spp. (Suckers), and the cyprinid genera *Richardsonius* and *Rhinichthys* (G. R. Smith 1981).

Glacial advances and retreats also impacted fish assemblages directly through extirpation or displacement into glacial refugia, followed by subsequent colonization of newly available habitats when glaciers retreated. At least five major glacial refugia, as well as various minor refugia, allowed the survival of organisms displaced by advancing ice (Fig. 1.8) (Flint 1971; Crossman & McAllister 1986; Cox & Moore 1993; Stamford & Taylor 2004). As a consequence, some northern fish assemblages have only been formed within the last 10,000 years and colonization of once glaciated areas is an ongoing process (Crossman & McAllister 1986; Lundberg et al. 2000). For example, species richness in formerly glaciated areas, as shown for Ontario, Canada, is related strongly to distance from glacial refugia and the time that colonization corridors have been free of ice (Mandrak 1995).

In central North America, the majority of colonizations of once glaciated areas occurred via the Mississippi Refugium (Fig. 1.8), contributing species to north-central Canada, the Hudson Bay drainage, and the Arctic Archipelago (Mandrak & Crossman 1992; Matthews 1998). Across Ontario, Canada, which was totally covered by the Wisconsinan glacial advance, 77 of 91 species for which glacial refugia are resolved colonized from the Mississippi Refugium, 18 from the Atlantic Refugium, and 2 from the Missouri Refugium (Mandrak & Crossman 1992). Most of the Ontario species (86) for which refugia could be identified survived the glacial advance in a single refugium, and only 5 had multiple refugia. Of the 21 common species limited to the Great Lakes and Nelson River (Hudson Bay

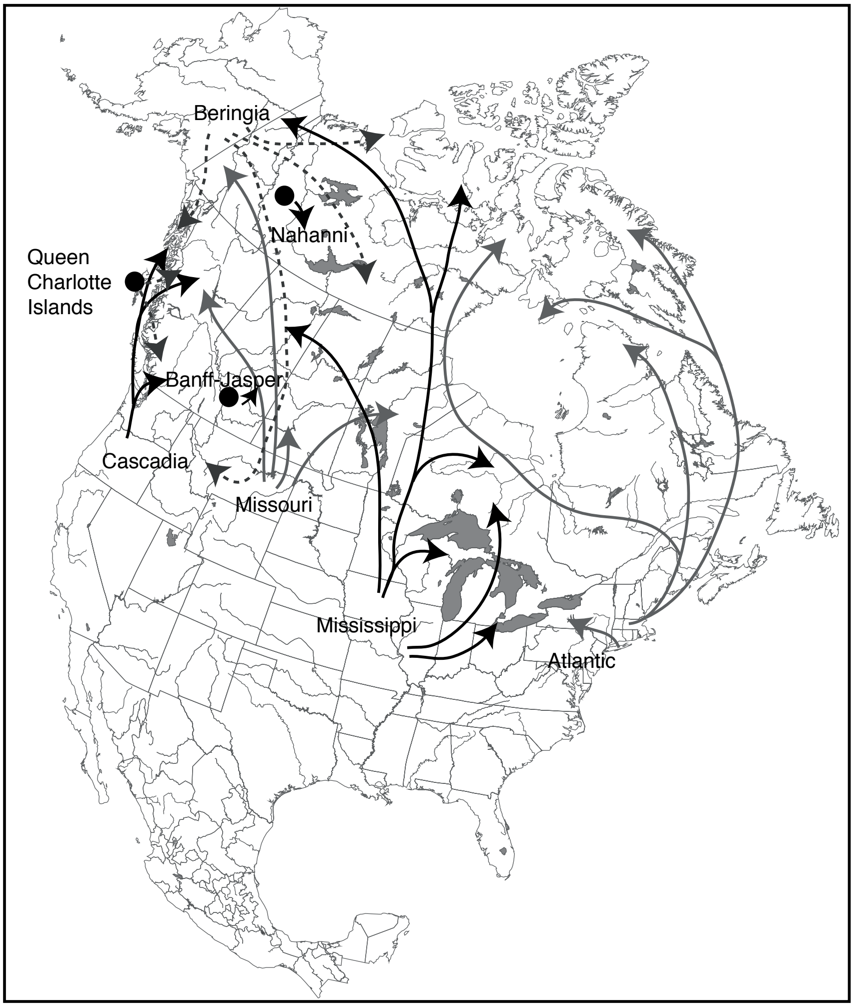

Figure 1.8. Glacial refugia during the Wisconsinan glacial advances and pathways of recolonization. Smaller refugia are indicated by closed circles. Based on data from McPhail & Lindsey (1970, 1986), Mandrak & Crossman (1992), Matthews (1998), McCusker et al. (2000), Smith et al. (2001), and Stamford & Taylor (2004).

drainage) watersheds, 14 originated from the Mississippi Refugium, 1 species originated from both the Mississippi and Atlantic Refugia, 1 species originated from the Atlantic Refugium, and 1 species originated from the Atlantic, Mississippi, and Missouri refugia (Fig. 1.8; Mandrak & Crossman 1992). Whether assemblages tended to move as groups of species or as individual species is unknown, although colonization likely occurred in waves of immigrants, when passageways from various refugia became free of ice.

Recolonization of New England and southeastern Canada by fishes from the Atlantic Refugium likely occurred initially via drainages in Connecticut because these drainages were the first to be fully free of ice, and a series of proglacial lakes and rivers forming within the Connecticut River Valley (extending from Connecticut through Massachusetts, New Hampshire, and Vermont) would have provided suitable habitats, dispersal routes, and subsequent access to more northern habitats. Glacial Lake Connecticut occupied the area of Long Island Sound from about 19,000–15,500 years ago, and Glacial Lake Hitchcock occupied the Connecticut River Valley about 18,000–12,000 years ago (Poppe et al. 2000; Benner et al. 2009). Based on trace fossils (e.g., tracks and traces in bottom sediments made by invertebrates and fishes), early recolonizers likely included species of *Salvelinus* and *Cottus*, which were present in Glacial Lake Hitchcock by 13,700 years ago (Benner et al. 2008, 2009). The Eastern Blacknose Dace (*Rhinichthys atratulus*) also recolonized proglacial habitats. The species initially recolonized eastern drainages in Connecticut (including the Connecticut River drainage) through a single founding event from a single Atlantic refugium in the early stages of deglaciation. Some 9,000 years later, a second colonization occurred in the more western Housatonic River drainage of Connecticut but not in the other two more eastern drainages (Connecticut and Thames Rivers). Consequently, Eastern Blacknose

Dace populations in the three major drainages of Connecticut are derived from at least two refugia and differ greatly in how long they have occupied the region (Tipton et al. 2011).

In western North America, four refugia (Beringia, Cascadia = Pacific, Mississippi, and Missouri) contributed to the formation of present fish assemblages. Times of faunal movement out of these refugia differed because of an earlier retreat of ice from coastal refugia and from the Missouri Refugium of the Great Plains compared with the Mississippi Refugium (McPhail & Lindsey 1970). Fish faunas of six hydroregions of Alaska each contain immigrants from the four principal refugia, although the contribution of the southwest Cascadia Refugium decreases from south to north and that of the Beringia Refugium decreases from north to south (Fig. 1.9; Morrow 1980; Oswood et al. 2000, using data from McPhail & Lindsey 1970). These examples suggest that fish assemblages in formerly glaciated regions experienced a step-like increase in colonizers over time as passage from the various refugia became possible and that western assemblages, like their northern counterparts, often contain species from multiple refugia.

Cooling associated with the Pleistocene resulted in a general southward displacement of terrestrial plants and animals outside of the areas of direct glacial impact (Pflieger 1971; Whitehead 1973; Pielou 1991). In watersheds that trended in a north-south direction, fish species also showed this pattern. Southward displacement likely was aided by a combination of increased stream discharge and changes in the character of streams in addition to cooler temperatures (Cross 1970; G. R. Smith 1981; Cross et al. 1986). For instance, species that today have a primarily northeastern or north-central distribution, such as the Redbelly Dace (*Chrosomus erythrogaster*), Northern Studfish, and Rainbow Darter (*Etheostoma caeruleum*), have disjunct populations as far south as Mississippi (Ross 2001) and the Redbelly Dace and Creek Chub (*Semotilus atromaculatus*) have disjunct populations in northeastern New Mexico (Pflieger 1971).

A general pattern of reduced species richness is associated with glaciated areas (Fig. 1.1); however, in some cases isolation stemming from glacial activity resulted in increased rates of speciation (e.g., Bernatchez et al. 1996). For instance, the Lake Whitefish (*Coregonus clupeaformis*) diverged into three genetically distinct races during isolation in the Beringia, Mississippi-Missouri, and Nahanni glacial refugia (Foote et al. 1992). In addition to coregonines, speciation in formerly glaciated areas occurred in other groups of fishes, including Smelts (*Osmerus* spp.), Sticklebacks (*Gasterosteus* spp.), whitefishes (*Prosopium* spp.), and chars (*Salvelinus* spp.) (Schluter & McPhail 1993).

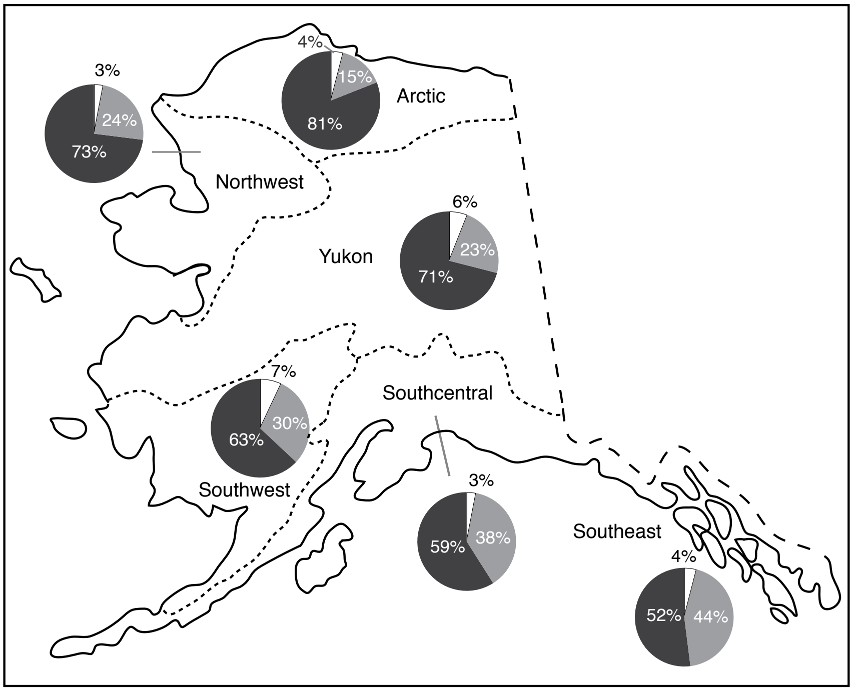

Figure 1.9. Contributions of three glacial refugia to the fish faunas of Alaskan hydroregions. Beringia—black; Cascadia—light gray; upper Mississippi—white (modified with permission from Oswood et al. 2000, Journal of the North American Benthological Society 19:405–418; copyright 2000 North American Benthological Society).

RESPONSES OF FISH ASSEMBLAGES TO LOCAL AND REGIONAL EFFECTS

We have shown that regional fish faunas are products of various and complex historical events, and that fish assemblages, like those of other biota (Jablonski & Sepkoski 1996), have undergone continual cycles of breakup and rearrangement over geological time. In this section we examine how the regional environmental characteristics, the regional fauna, habitat type, and habitat quality influence local fish assemblages. In doing so, we are making the transition from the realms of biogeography and evolutionary ecology to that of community ecology (see Keddy & Weiher 2001).

Fish assemblages are influenced by factors operating at the local scale (e.g., physical habitat, predators, competitors) and by regional effects including climate, elevation, geographic location, and the regional fish fauna of which they are part (Fig. 1.2). Hugueny et al. (2010) proposed a broad framework by which to view fish communities, integrating across scales from historical and biogeographic factors to interactions among species in local communities and including regional synchrony in community changes. To understand relationships of species or functional groups to environmental variables, one must recognize that the presence of a particular kind of fish in a habitat may vary spatially and temporally on annual, seasonal, or daily scales and that such variation often is compounded by changes in life history stage. Within North American freshwater fishes, the duration spent in a particular habitat can range from species that remain in the same general habitat throughout their entire lifespan, as in certain riffle-inhabiting darters such as the Orangebelly Darter (*Etheostoma radiosum*) (Scalet 1973) and Mottled Sculpin (*Cottus bairdi*) (Petty & Grossman 1996), or the extreme case of the Devils Hole Pupfish (*Cyprinodon diabolis*), which is restricted to Devils Hole, a 3 m × 20 m pool in the Death Valley system (Miller 1948; Deacon & Williams 1991), to those that move seasonally among habitats for purposes of reproduction, such as spawning migrations of catostomid fishes from large rivers into headwater streams (e.g., Curry & Spacie 1984), to long-distance migration hundreds or thousands of kilometers shown by diadromous fishes such as Sturgeons, Herrings, and Freshwater Eels (Anguillidae) (Heise et al. 2005; Helfman et al. 2009).

Although we use it here in a general way, the term "habitat" has various meanings and the significance of these meanings has garnered considerable debate (e.g., Ryder & Kerr 1989), generally relating to the distinction between habitat and environment. A current view is that habitat comprises the localized structured component that acts as a template for organisms, and environment is the sum of the biotic and abiotic surroundings, including habitat and other organisms (Peterson 2003). Habitat includes both static (i.e., substratum characteristics) and dynamic (i.e., water-column characteristics) components, and the extent of suitable habitat is defined by the degree of overlap between suitable dynamic and static components (i.e., suitable static habitat alone is not sufficient if suitable dynamic habitat does not also occur) (Peterson et al. 2007).

Local and Regional Environmental Effects on Assemblages

Various models have been proposed relating large-scale, regional factors (e.g., geology, climate, rainfall, elevation) to the primary structure of assemblages (e.g., species presence, relative abundance) or to emergent assemblage structure (e.g., species richness, diversity, assemblage complexity, trophic relationships) (Marsh-Matthews & Matthews 2000). A recent evaluation of temporal changes in fish assemblages of three large Great Plains river basins emphasizes the importance of understanding the comprehensive and comparative impacts of broad regional factors, such as groundwater withdrawal, sedimentation, habitat fragmentation, and invasive species, if long-term changes in local and regional fish communities are to be fully appreciated (Gido et al. 2010a). Approaches relating local habitat features to fish assemblages are treated in the subsection on habitat type and quality.

Three conceptual models historically used to predict emergent structure in lotic assemblages from basic ecological principles are the habitat template (Southwood 1977, 1988), landscape filters (Poff 1997), and the river continuum concept (Vannote et al. 1980) (see summary by Goldstein & Meador 2004). Frimpong & Angermeier (2010) suggested that incorporating traits of individual species, a trait-based approach, can profitably combine knowledge about the basic biology of individual species with environmental conditions to provide a robust view of success of individual species in local habitats or the composition of a local assemblage or functional groups. Other traits, in addition to those internal to a fish species, might strongly relate to the role of that species in an ecosystem. For example, McIntyre & Flecker (2010) highlighted the fact that fish species differ markedly in the elemental composition of their bodies (stoichiometry) and thus, in the nutrient ratios of their waste products, making species identity in an assemblage an important factor in the effects of those fish on the ecosystem.

In the habitat template model, the habitat is suggested as a template providing a predictive pattern for the evolutionary assembly of communities and life history traits thereof, much like the periodic table of elements in chemistry (Southwood 1977, 1988). An important assumption is that current organismal traits match current environmental conditions, which is not necessarily the case (see origin and age of North American fish families section). To test predictions of the habitat template model, Townsend & Hildrew (1994) used a large data set from the River Rhône drainage, France. They focused on two axes, temporal habitat heterogeneity (a measure of the frequency of disturbance) and spatial heterogeneity (a measure of the availability of refugia), in developing predictions of how species traits would respond to the habitat template. For instance, the species trait of body size should decrease in environments with low spatial heterogeneity and high temporal heterogeneity (i.e., unstable environments) and be large or small in environments with high spatial heterogeneity and low temporal heterogeneity (i.e., stable environments). Similarly, lifespan should be short in unstable environments and long or short in stable environments. Tests of these and other predictions based on 13 taxonomic groups of plants and animals from the Rhône River drainage resulted in only mixed support for the habitat template model and support for fishes was totally lacking (Resh et al. 1994). The large data set used to test the predictions might have had methodological limitations that precluded a fair test of the model (Resh et al. 1994).

Studies of U.S. midwestern streams (Poff & Allan 1995) and comparisons of functional convergence between European and eastern North American fish assemblages (Lamouroux et al. 2002) offer somewhat stronger support for the habitat template model. For instance, two predictions of the habitat template model, that variable habitats should contain more resource generalists and that nonvarying habitats should contain more specialists, was supported for midwestern U.S. stream fish assemblages (Poff & Allan 1995). Variables used to characterize habitat variability included flow predictability and variation, base flow stability, and frequency of spates (Poff & Allen 1995). Ecological traits of species, including body size, longevity, fecundity, water-column position, body shape, and swimming ability responded similarly to the physical habitat template, determined by Froude number (ratio of current velocity and water depth), in France and Virginia (Lamouroux et al. 2002). Even though this shows predictive ability of the habitat template model, the amount of explained variation was generally <50%.

Flow predictability, especially in the arid western United States, could be considered one important component of a habitat template model. In particular, Turner et al. (2010) emphasized the importance of consistent coupling of high and low flows relative to phenology of reproduction by fishes to match availability of larval foods. If, in a future climate, changes in snowmelt or the monsoon season have the effect of making high and low flows in snowmelt rivers less predictable, this could eliminate discharge cues that many species at present rely on for successful reproduction (Turner et al. 2010).

Poff (1997) proposed that functional attributes of species in communities are shaped by a hierarchical series of landscape filters that include both physicochemical and biotic factors. A community is thus made up of species possessing the appropriate ecological shapes to have passed through the filters. The heuristic model we are using (Fig. 1.2) is similar to this approach. Key elements are categorical niches, defined as discrete levels of species' requirements along a given resource axis, and categorical filters, defined as the strength or resistance of a filter in allowing species to pass through it. The combination of categorical filter strength with the categorical niche determines the probabilities for a species to pass through a given filter. Analysis of a large data set of fishes from the eastern United States revealed that functional and morphological characteristics of species generally fit predictions of Poff's landscape filter (Goldstein & Meador 2004). For instance, the landscape model prediction that fish morphology would be best predicted by local factors such as hydraulic stress was supported. Frimpong & Angermeier (2010) expanded the assessment of Goldstein & Meador (2004) to group traits exhibited by species into multi-trait syndromes (i.e., phenomena and characteristics that often occur together so that the presence of one or more traits suggests the presence of others).

The role of landscape, or factors by which landscape factors affect local fish assemblages, can be extremely complex. Infante & Allan (2010) emphasized the role of intermediate factors that connected landscape phenomena to the local fishes and the relative influence of natural versus anthropogenic landscape factors on the fishes. Their study of watersheds in the Huron and Raisin River basins, Michigan, showed that, overall, natural landscape factors like geology and catchment area influenced fish assemblages more strongly than did land-use factors (Infante & Allan 2010).

The river continuum model emphasizes continuity with gradual changes in species occurrence and functional groups from headwaters to downstream reaches (Vannote et al. 1980), although the original paper had only limited information on fishes. Predictions of fish assemblage composition by the river continuum model are limited primarily to trophic groups and are based on food resources available in small, medium, and large streams. Food resources in small streams would be primarily terrestrial invertebrates with less importance of aquatic invertebrates or fishes as prey; medium streams should offer more aquatic prey, both insects and fishes; large streams should provide increased amounts of autochthonous production. Recent work on a forested, northern California watershed further documents the presence of longitudinal gradients in physical factors that can then influence biological components (Finlay et al. 2011). As solar insolation increases with channel width, carbon from instream primary production also increases, coincident with a drop in the input of terrestrial carbon. The strength of such gradients is perhaps lessened in streams that are not forested.

Numerous studies have examined variation in species composition or functional groups along longitudinal gradients in streams (e.g., Shelford 1911; Kuehne 1962; Sheldon 1968; Schlosser 1982, 1987; Roberts & Hitt 2010). Species richness and the number of functional groups tend to increase with stream size, at least for small- to moderate-sized streams, although changes in faunas are generally gradual and, with few exceptions (Matthews 1998), do not closely correspond with stream order (a measure of stream size based on branching patterns, Horton 1945; Strahler 1957) (Matthews 1986a). Predictions of changes in functional groups, such as fewer insect predators and more planktivores and detritivores with increasing stream size, generally are supported (Goldstein & Meador 2004).

Local and Regional Faunal Effects on Assemblages

Regional species composition, in addition to regional characteristics of the physical environment, also impacts fish assemblages. One can consider a local area to be saturated with species and thus resistant to the addition of new elements, regardless of the size of the regional fauna, or to be influenced by the regional fauna such that local species richness increases relative to regional richness (summarized by Ricklefs 1987; Cornell & Lawton 1992). The question is to what degree local fish assemblages are determined by processes acting within the local area versus processes operating at a regional level. Asymptotic relationships between local and regional species diversity (i.e., saturation) suggest the primacy of local control over assemblages; in contrast, if the relationship remains linear (i.e., unsaturated), then local processes would be subordinate to the effect of the regional species pool (Ricklefs 1987). At the same time, local assemblages obviously affect the regional species pool, creating a chicken-and-egg problem (i.e., which happened first or caused the other to happen) (Cornell & Lawton 1992).

In Virginia streams, regional diversity generally explained more of the variation in local native fish assemblages than did local variables, but local variables also showed some, albeit reduced, explanatory power with the most important being habitat complexity (Angermeier & Winston 1998). A graph of local species richness at the collecting site versus regional richness at the level of drainage is suggestive of an asymptote, given the low slope, an intercept significantly >0, and the premise that local richness cannot logically exceed regional richness and so should originate at 0 (indicated by the dotted line in Fig. 1.10). At a local scale, however, diversity in pools was related strongly to diversity at collecting sites (a site included three or more habitat units such as pools or riffles), indicating that the local habitats (pools) were not saturated (Fig. 1.10). The number of local introduced species was related positively to the regional number of introduced species at all regional scales, and in contrast to native species, showed no evidence of saturation. In addition, the number of native fish species did not influence the number of non-native species, suggesting that high native fish diversity does not preclude invasion by non-native fishes.

The strong influence of regional compared with local factors also is evident in lakes. Fish faunas of watersheds within the Laurentian Great Lakes were impacted by the effect of large-scale regional processes reflective of post-glacial dispersal or climate but were much less related to measures of environmental similarity (e.g., lake depth, area, and pH), although such factors likely have some role in affecting species composition (Jackson & Harvey 1989). In a comparison of small lakes in Wisconsin and Finland, species richness in individual lakes was related to regional species richness, but local richness reached an asymptote, suggesting that individual lake faunas become saturated with species (Tonn et al. 1990; Fig. 1.10).

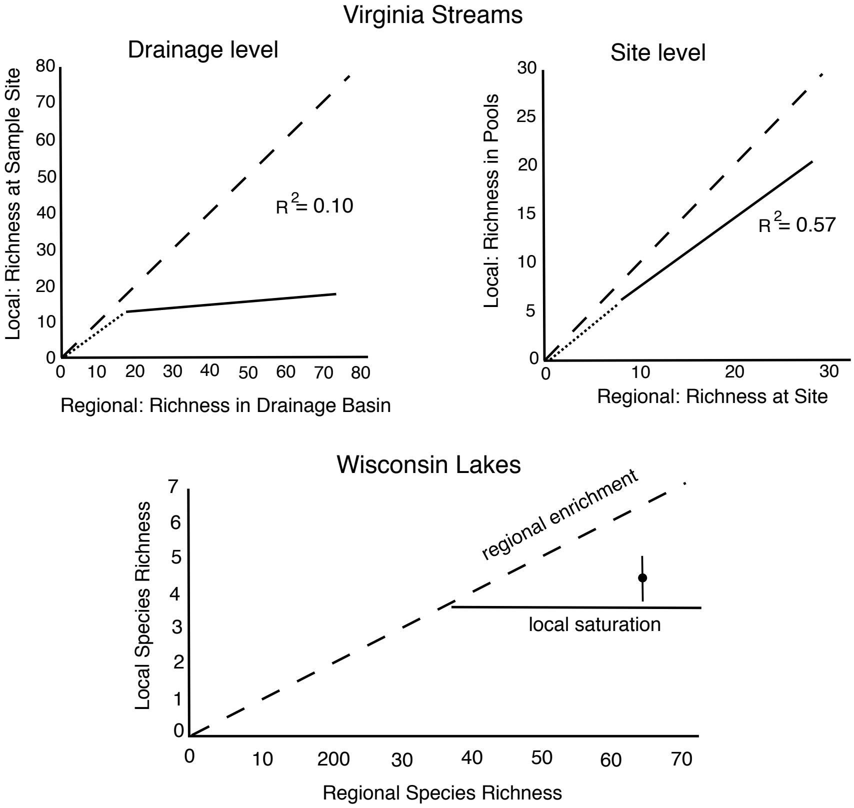

Figure 1.10. The relationship between native fish diversity of local assemblages to regional fish diversity in Virginia streams at the drainage and local scales (based on Angermeier & Winston 1998) and Wisconsin lakes (based on Tonn et al. 1990). Dashed lines indicate a hypothetical direct relationship between regional and local diversity; for Virginia streams, solid lines indicate actual relationships between regional and local diversity; dotted lines indicate extrapolation of local diversity to 0. The closed circle and vertical line indicate the mean and 95% confidence interval of local species richness for Wisconsin lakes. See text for further explanation.

Regional factors alone, however, could not explain local species composition because biotic factors, particularly the presence of large predators, also influenced species composition. Predator composition, lake morphometry, and winter oxygen levels also affected the structure of fish assemblages in small Wisconsin lakes (Tonn & Magnuson 1982).

These studies all suggest a general, but highly variable, link between regional and local species richness. In contrast, in a study of the Interior Highland region (Ozark and Ouachita Mountains, Arkansas, Oklahoma, Missouri, and Kansas), regional (river basin) fish species richness accounted only marginally for species richness at local sites over all species, and the regional-local species richness relationship was nonexistent within the Cyprinidae and Percidae. Overall, the number of species in local assemblages varied greatly within basins, suggesting a lack of strong regional-local effects and the greater influence of local physical or biotic factors on local diversity (Matthews & Robison 1998). Similarly, for midwestern stream fishes (65 sites, 13 drainages, Nebraska and Iowa south to Texas), local factors affected species richness more than the overall size of the regional species pool (Marsh-Matthews & Matthews 2000). Even so, in contrast to emergent assemblage properties (i.e., species richness), primary assemblage structure (i.e., the occurrence of particular species) was influenced strongly by broad geographic factors, primarily latitude, reflective of the fact that many species have restricted north-south distributions (Conner & Suttkus 1986; Cross et al. 1986). Similarly, in Texas stream fish assemblages, regional environmental factors and the regional species pool were important in affecting species composition of local assemblages (Hoeinghaus et al. 2007); however, functional group response was influenced more strongly by local environmental and biotic factors.

Regional and historic filters (see Tonn et al. 1990) clearly can have a major influence on local assemblages and in some cases, especially southeastern streams and northern lakes, the richness of local fish assemblages is affected strongly by regional diversity. Species composition also can be greatly influenced by large-scale factors such as latitude, zoogeographic region, divisions between major river basins, and stream size (e.g., Swift et al. 1986; Hitt & Angermeier 2011). Nevertheless, not all assemblages show a relationship between regional and local diversity, as evidenced by harsh midwestern streams and speciose upland streams.

Effect of Habitat Type and Quality

Current velocity, water depth, water quality, bottom type, food availability, and structure are all important factors affecting habitat selection by fishes and thus have substantial impacts on assemblage structure. Within limits set by the regional species pool, the occurrences of particular species, and thus the composition of a local assemblage, are dictated to a large degree by the type and quality of the local habitat and the surrounding environment, including riparian zones.

At the level of stream reaches (i.e., lengths of streams including several riffle-pool sequences), hydrologic variables, and in particular Froude number, explained ≤50% of the variance in functional traits of stream fish assemblages in both eastern North America and Europe (Lamouroux et al. 2002). In the upper Red River, Oklahoma, predictability of fish assemblages also was based on environmental gradients; however, in this physically harsh, often saline system the conductivity gradient had the most predictive power (Taylor et al. 1993). For midwestern stream fishes, local aquatic habitat variables explained a small but significant amount of variation in species richness (14%) and assemblage complexity (15%) (Marsh-Matthews & Matthews 2000).

On a finer scale, species differences also occur between shallow runs or riffles and deeper pool habitats (Schlosser 1987) with the differences more pronounced in large versus small streams (Taylor 2000). Schlosser (1987) developed a conceptual framework of processes affecting fish assemblages along a gradient of pool development, habitat volume, and habitat heterogeneity. He proposed that fish assemblages in upstream, shallow areas are driven primarily by high variability in physical factors such as droughts and floods, but assemblages in downstream areas containing environmentally complex, deep pools are less variable and driven more by biotic interactions. In the Little River, Oklahoma, patterns of faunal similarities among 74 stream sites were different between adjacent pool and riffle assemblages, suggesting that the 2 assemblages responded differently to environmental factors (Taylor 2000). Pools almost always had more species than riffles, but riffle assemblages tended to be more similar to pool assemblages in smaller streams. In an upland stream reach of the Illinois River, Oklahoma, most species shifted from backwater pools early in life to pools or riffles as they increased in size (Bart 1989). Riffles were not used to any great extent by young (only 30% of riffle species occurred in the riffles as young). In an even smaller headwater stream in the same drainage (Gelwick 1990), more species occurred in pools (21) than in riffles (11), and only 3 species (Slender Madtom, *Noturus exilis*; Fantail Darter, *Etheostoma flabellare*; and Banded Sculpin) were exclusive to riffles. Pool and to a lesser extent riffle assemblages showed some changes longitudinally over the 6 km stream section. In apparent contrast with studies in larger streams, riffles seemed to function more as supplemental habitats or as refuges from predation for juvenile individuals of taxa found in pools. Riffle taxa shifted into pools during droughts or floods (Gelwick 1990). Thus, the use of pool and riffle habitats by fishes varies relative to stream size and hydrologic conditions. Sizes of fishes also vary among riffles, runs, and pools with larger individuals of the same species, and also larger species, occupying pools (Mahon & Portt 1985). This is part of the overall phenomenon of bigger fishes being present in deeper habitat that is demonstrated for stream fishes on a variety of scales and locations (e.g., Power 1987; Gorman 1987; Harvey & Stewart 1991; see predation subsection).

These and other studies show that some species are restricted to riffle habitats. An example of a specialized riffle inhabitant is the Bayou Darter (*Nothonotus rubrum*) of Mississippi, which shows strong selection not only for riffle habitats but also for riffles with certain characteristics. Bayou Darters occur in shallow riffles characterized by current speeds averaging 79 cm/s and having a coarse (mean particle size 16–32 mm), firm substratum (Ross et al. 1990, 1992). Individual fish are rarely encountered outside of favorable riffle habitats, although larval stages do move downstream in the drift (Slack et al. 2004). In the winter, selection for coarse structure in riffles increases when fish are energetically constrained to seek out refuges from high current speeds and preferentially choose larger over smaller refuges (Ross et al. 1992). Further, as riffle habitats are created (in this case by headward erosion), the Bayou Darter has expanded its range into more upstream reaches (Ross et al. 2001).

Even within riffles, fish species may use habitats quite differently, as shown by studies of habitat partitioning among riffle-dwelling fishes. For example, five species of darters within the genus *Etheostoma* (Greenside Darter, *E. blennioides*; Rainbow Darter; Orangethroat Darter, *E. spectabile*; Missouri Saddled Darter, *E. tetrazonum*; and Banded Darter, *E. zonale*) differed in their occupation of riffle habitats in streams of the Ozark upland region, primarily along a gradient of association with submerged and emergent vegetation and less so on the basis of substratum size, water depth, or current speed. Orangethroat Darters typically occurred on riffles lacking vegetation, but Rainbow Darters were associated strongly with emergent vegetation. Species also segregated relative to stream size with Missouri Saddled Darters found more in riffles of large than small streams (White & Aspinwall 1984). Within a single riffle in the Roanoke River, Virginia, microhabitats of three darter species (Fantail Darter; Riverweed Darter, *Etheostoma podostemone*; and Roanoke Logperch, *Percina roanoka*) showed distinct differences in water flow and depth of microhabitats (Matthews et al. 1982a). The differences in current speeds selected in the riffles corresponded to differences in morphology, behavior, and the ability to tolerate exposure to flow for two of the species, the Fantail Darter and Roanoke Logperch (Matthews 1985).

Underwater observations are used to study habitat use of fishes within a short stream reach, usually consisting of a pool, run, and riffle. For instance, in a fish assemblage in a southern Appalachian stream, benthic and water-column fishes generally used habitat non-randomly (Grossman & Ratajczak 1998). The habitat gradient along which fishes primarily differed contrasted high-velocity, erosional areas with low-velocity, depositional areas. In addition, some species shifted in microhabitat use both seasonally and ontogenetically. Large individuals of water-column species, such as the Warpaint Shiner (*Luxilus coccogenis*), River Chub (*Nocomis micropogon*), Rainbow Trout (*Oncorhynchus mykiss*), and Creek Chub, tended to occupy deeper microhabitats than small individuals. Large individuals of benthic species, such as the Longnose Dace (*Rhinichthys cataractae*) and Mottled Sculpin, occurred closer to shelter and in higher current velocities than did small individuals. In wide pools of Baron Fork, Oklahoma, small, juvenile Central Stonerollers (*Campostoma anomalum pullum*) are restricted to shallow pool margins, but large individuals occur in deep water, mid-pool areas (WJM pers. obs.). In a montane stream in Idaho, both Cutthroat Trout (*Oncorhynchus clarkii*) and Bull Trout (*Salvelinus confluentus*) were non-random in macrohabitat use, selecting pools over riffles (Bonneau & Scarnecchia 1998).

Non-random habitat use also is well documented in lentic systems, where water depth and distance from shore, submerged aquatic vegetation, and vertical water-column position are often important axes of separation (Moyle 1973; Werner et al. 1983ab; Ross 1986; Benson & Magnuson 1992). In small Michigan lakes, species differed primarily by habitat (Werner et al. 1977). The shallow, vegetated littoral zone was used primarily by juvenile centrarchids, such as small Bluegills (*Lepomis macrochirus*) and various cyprinids, but larger Bluegills, Black Crappies (*Pomoxis nigromaculatus*), and Largemouth Bass (*Micropterus salmoides*) occurred in deeper, more open areas. Fishes also segregated vertically. For example, Blackchin Shiners (*Notropis heterodon*) used the upper water column, but Blacknose Shiners (*Notropis heterolepis*) were more associated with the bottom. Similarly in Florida lakes, the fish assemblage responded strongly and positively to the location and type of submerged aquatic vegetation, and fishes were uncommon outside of the vegetated areas. In addition, Bluegills tended to increase in size with increasing water depth, although Largemouth Bass, which were concentrated just outside the vegetated areas, did not show size increases with depth (Werner et al. 1978). Fish species also segregated vertically within the water column, a pattern documented in other studies of lake fishes (Keast & Fox 1992).

The use of habitats by fishes in both lentic and lotic habitats may vary temporally over a 24-h period and also seasonally (including shifts due to different life history stages). Studies of diel shifts in habitat use are more common in lakes than in streams and often show regular patterns of movement of fishes into and out of specific habitats, but studies of seasonal changes in habitat are more common in streams. For instance, all sizes of Bluegills and small Largemouth Bass in a northern lake tended to move inshore and higher up in the water column at dusk (Werner et al. 1977). In another northern lake, striking changes also occurred in abundance of fishes in particular habitats between day and night samples, and the patterns varied somewhat by month. The changes were not so much shifts in assemblage composition as shifts in relative abundances. In that study, the night sampling occurred between 2200 and 2400 h and divers used lights to locate fishes (Keast et al. 1978). Bluegills tended to move to more exposed areas to forage; in addition, individual Bluegills and Pumpkinseeds (*Lepomis gibbosus*) were observed motionless on the bottom in shallow water (<1 m). Day-night changes in distribution also occurred for Rock Bass (*Ambloplites rupestris*), Black Crappies, and Brown Bullheads (*Ameiurus nebulosus*). Rock Bass shifted out of rocky areas to feed over sand and gravel, Black Crappies moved into deeper water to feed at night, and some Brown Bullheads moved from deeper to shallower water at night. Significant changes in catch rates of centrarchids also occurred in trap nets set just outside of the vegetation line in a small Ohio lake (Shoup et al. 2004). To some extent, the diurnal-nocturnal shifts in habitat use of North American lake fishes correspond to the changeover observed on tropical reefs (Helfman 1979, 1981). Diurnally active planktivorous fishes, such as Bluegills and Yellow Perch (*Perca flavescens*), moved out of the water column at night and into closer association with cover or found resting areas near the bottom; smaller fishes tended to show greater affiliation with cover. Some of these diurnally active fishes (Mimic Shiner, *Notropis volucellus*; Banded Killifish, *Fundulus diaphanus*; Smallmouth Bass, *Micropterus dolomieu*; and Yellow Perch) became motionless on or near the bottom and moved little at night. Nocturnally active fishes, such as the Golden Shiner (*Notemigonus crysoleucas*), Rock Bass, and Brown Bullhead, moved from sheltering to foraging areas and initiated feeding as light levels dropped. Another cyprinid species, the Northern Redbelly Dace (*Chrosomus eos*), also showed diel movement, shifting from shallow, vegetated littoral zones during the day to the offshore, pelagic zone over deeper water at dusk and dawn (Naud & Magnan 1988). The movement seems primarily associated with the concentrations of their cladoceran prey.

Patterns of diel movement also may vary with lake size or water conditions. For instance, benthic and water-column species in the Great Lakes move from deeper regions to depths of 0–30 m at night, often seeking cover within boulder fields or in submerged aquatic vegetation (Emery 1978). In Lake Texoma, a large impoundment on the Red River, Oklahoma and Texas, the occurrence of fishes such as the Mississippi Silverside (*Menidia audens*) in the shallow littoral zone may vary on a daily basis as a function of wind-driven wave height (Matthews 1998). Also in Lake Texoma, the diel occurrence of fishes in littoral zone habitats differed greatly during both the summer and winter. Gizzard Shad (*Dorosoma cepedianum*), Mississippi Silversides, River Carpsuckers (*Carpiodes carpio*), and various minnow species were more abundant during the day; night samples yielded more Freshwater Drum (*Aplodinotus grunniens*), White Crappies (*Pomoxis annularis*), Striped Bass (*Morone saxatilis*), and White Bass (*Morone chrysops*) (Hubbs 1984; Matthews 1986b). As some of these studies indicate, diel vertical movements are especially prevalent in large lakes and often have the pattern of movement into surface waters at dusk with a return to deep water at dawn.

Water clarity also may influence diel changes in habitat. As clarity decreases, vulnerability of prey fishes to visually oriented predators also decreases. The low water clarity of Pelican Lake, Nebraska, and its effect on visual predators such as the Northern Pike (*Esox lucius*), likely was responsible for the absence of diel habitat shifts in Bluegills (Paukert & Willis 2002).

Diel changes in habitat use are somewhat less studied in streams compared with lakes; however, the lack of information on habitat shifts of fishes in streams is likely due more to the difficulty of observing fishes in streams than an actual absence of diel movement of fishes. In fact, although not as prevalent in temperate compared to tropical streams, diel turnover of fish assemblages occupying sandy shoals may be a general phenomenon in lotic systems (Roach & Winemiller 2011).

Diel habitat shifts vary among stream fishes within an assemblage. In a small southeastern U.S. stream, centrarchids tended to remain in the same general habitats over a 24-h period, whereas cyprinids, as shown above for lake inhabitants, shifted from deeper daytime habitats to shallower areas with lower water velocities at night (Ensign & Leonard 2004). In a small blackwater stream in Mississippi, cyprinids such as the Blacktail Shiner (*Cyprinella venusta*) shifted from deep areas with high current speeds during the day to shallow, slow areas at night where they lay motionless on the bottom (STR unpubl. data). A similar pattern occurred for the Duskystripe Shiner (*Luxilus pilsbryi*) in Ozark upland streams (WJM pers. obs.). Some darter species, especially *Percina* spp. (Tangerine Darter, *P. aurantiaca*; Gilt Darter; Logperch, *P. caprodes*; Blotchside Logperch, *P. burtoni*; and Sickle Darter, *P. williamsi*), increased their use of rock cover at night, but large individuals of the Greenside Darter tended to occur more on top of rocks at night than during the day. Other species of *Etheostoma* (Redline Darter, *E. rufilineatum*; Wounded Darter, *E. vulneratum*; and Snubnose Darter, *E. simoterum*) tended to be associated with rock cover irrespective of time of day (Greenberg 1991). In a montane stream, juvenile Bull Trout and Cutthroat Trout increased use of shallow water at night. Both species also tended to move into lower-velocity habitats at night, irrespective of depth (Bonneau & Scarnecchia 1998). Age-0 Brown Trout (*Salmo trutta*) also moved into shallower habitats with lowered current velocity at night with the extent of shallow habitat use decreasing as fish grew in size (Hubert et al. 1994). In Black Creek, a southeastern U.S. stream, the Speckled Madtom (*Noturus leptacanthus*) moved from daytime shelter among submerged aquatic vegetation (primarily *Sparganium americanum*) or other structures to active foraging in shallow water at night (Clark 1978). Other madtom species, including the Tadpole Madtom (*Noturus gyrinus*), Black Madtom (*Noturus funebris*), Least Madtom (*Noturus hildebrandi*), and Brown Madtom (*Noturus phaeus*), also show daytime sheltering and increased nocturnal movement that is primarily associated with foraging

(Clark 1978; Wilkins 1992; Chan & Parsons 2000). Similarly, in a study along the Brazos River, Texas, Blue Catfish and Channel Catfish as well as Flathead Catfish (*Pylodictis olivaris*) moved from resting areas in deeper water during the day into shallow, sandy areas at night for foraging (Roach & Winemiller 2011).

In general, these studies show that many stream fishes tend to increase their use of shallow habitats with low current velocity at night, although some species do not show any apparent diel shifts in habitat use. Visual surveys by snorkeling, used in most observational studies, have the potential of introducing biases in habitat-use assessment. For instance, studies of diel changes in habitat depth of Bull Trout may reflect the increased tendency of fish to retreat from shallow habitats during the day in the presence of snorkelers compared with at night, resulting in an overestimation of deeper habitat use during the day (Banish et al. 2008).

In winter, stream fishes often occupy lower-velocity habitats, show increased association with refuges from strong currents, or both. This includes sheltering behind large objects or occupying the interstices of pebble, cobble, and boulder substrata. Examples include cyprinids such as the Blacknose Dace (*Rhinichthys atratulus*) (Cunjack & Power 1986), percids such as the Bayou Darter (Ross et al. 1992), and salmonids, including the Bull Trout and Cutthroat Trout (Bonneau & Scarnecchia 1998), Rainbow Trout (Baltz et al. 1991), and Atlantic Salmon (*Salmo salar*) (Cunjak 1988). In a channelized stream in Mississippi where natural structure was limited, fishes showed increased association with constructed microhabitats following a winter storm and a rapid decrease in water temperature (Warren et al. 2009). In the main channel of Baron Fork, Oklahoma, large schools of adult Central Stonerollers decrease activity and abandon flowing water in the winter and move into quiet lateral habitats such as spring seeps or small tributaries to the main channel (WJM pers. obs.). During winter seine collections, one consequence of winter habitat shifts of fishes is to find long reaches of streams without cyprinids and then to encounter large mixed-species groups in deep pools (WJM, STR pers. obs.). Fishes also show seasonal habitat shifts in lakes. For instance, in Michigan, Bluegills, Pumpkinseeds, shiner species (principally the genera *Notemigonus* and *Notropis*), and Yellow Perch moved from generally shallow, littoral areas to deep areas of the littoral. In particular, Bluegills overwintered in deep areas of the littoral that supported dense stands of upright vegetation such as *Potamogeton* (Hall & Werner 1977).

Spatial changes in habitat use also are influenced strongly by life history stage. In flowing water the ability to swim against the current is affected directly by body size. As a consequence, larval and juvenile stages tend to occur in edge habitats where current flow is absent or minimal, although habitat selection can be altered greatly by predation. Such habitats are also generally shallower and warmer than mainstream areas and may offer protection from aquatic predators for juvenile fishes. Similar patterns occur in lentic habitats where early life history stages of fishes tend to occur in shallow, sometimes vegetated, shoreline habitats (e.g., Hall & Werner 1977; Keast et al. 1978). Because of the strong impact of predation on habitat use, ontogenetic habitat shifts are discussed further in the interactions within fish assemblages section.

The selection of habitats by fishes is influenced strongly by the interaction between growth (which integrates temperature, food level, and other environmental costs and benefits) and the risk of mortality (Railsback & Harvey 2002). Given the size-structured nature of fish populations, the defining characters of habitat suitability change ontogenetically. For example, a bioenergetics model appeared best to explain vertical movement patterns of juvenile Sockeye Salmon (*Oncorhynchus nerka*) in British Columbia lakes (Brett 1971). Juveniles occupied the cold hypolimnion during the day and migrated into surface waters at dusk and again at dawn to feed on zooplankton. Energy assimilation should be most efficient by feeding in the relatively warm surface water and then digesting prey in deeper, colder water (Brett 1971). Although Brett discounted the role of predation in contributing to the vertical migration, later work suggests that the vertical migration of Sockeye Salmon, and many other lacustrine species, is driven primarily by balancing risk of mortality with energetic gain, and that for visually oriented predator-prey systems, this may reach an optimum point for juvenile fishes, termed an "anti-predation window," at dawn and dusk (Clark & Levy 1988). At these times, light intensities allow juvenile Sockeye Salmon to detect their prey, but they are at the same time less visible to their own predators.

Models based on optimal foraging theory (i.e., the best return of energy for time and energy spent foraging, prey kind and quality, and prey capture success) can successfully predict habitat use in lentic and lotic systems. In a pond section without large piscivores, three size classes of Bluegills all shifted their foraging habitats (determined from dietary analyses) over time from open water to sediment in accordance with predictions of optimal energy returns (Fig. 1.11a) (Werner et al. 1983a). For large Bluegills,

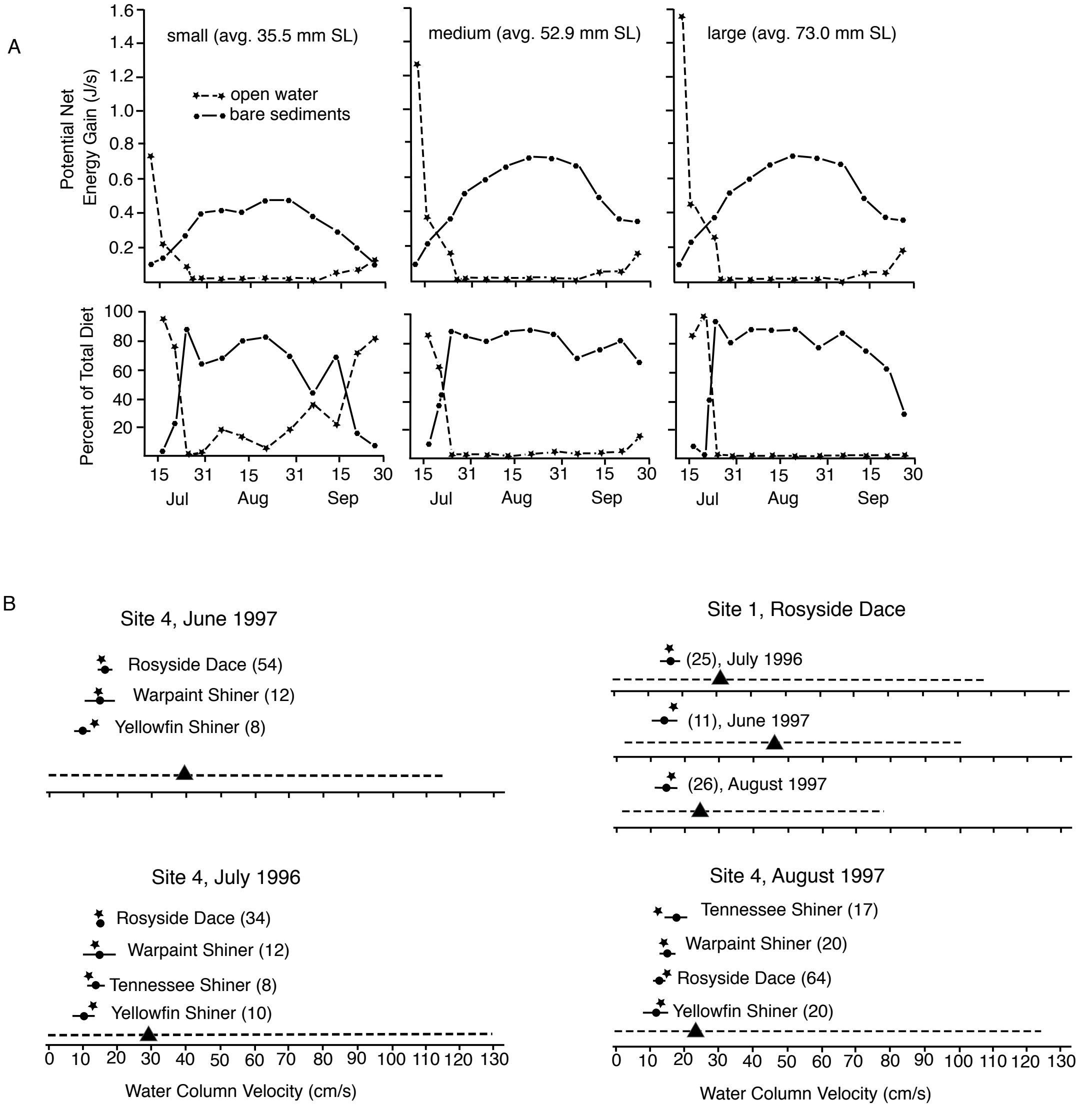

Figure 1.11. Predictions and tests of optimal foraging models for lentic and lotic fishes. (A) Habitat shifts in three size groups of Bluegills (*Lepomis macrochirus*), as shown by diet, relative to predictions of net energy gain and percentage of total diet. The top three panels show potential net energy gain in open water and bare sediment habitats; the lower three panels show actual foraging locations based on the observed diet. Use of vegetation was low for all three size classes and is not shown (modified with permission from Werner et al. 1983a; copyright 2000 Ecological Society of America). (B) Observed focal point velocities for four minnow species (closed circles = means, lines = 95% CI), predicted optimal velocities (stars), the grand mean of water column velocity measurements (triangles), and the range of available water column velocities (dashed line). Sample sizes are in parentheses; data taken from sites 1 and 4, Coweeta Creek, North Carolina (redrawn from Grossman et al. 2002).

essentially the same shifts occurred in the presence of predators. In Coweeta Creek, a small stream in the Appalachian Mountains, North Carolina, an optimal foraging model predicted habitat use, as defined by focal current velocity, in 79% of the cases for four species of drift-feeding minnows over two sites and four time periods (Fig. 1.11b) (Grossman et al. 2002). In the three instances where model prediction was outside of the 95% confidence interval of current speed, predicted values were within 2 cm/s, and this in a stream where velocities ranged from 0 to 128 cm/s.

Water temperature is a major factor in habitat selection by fishes (e.g., Beitinger et al. 1975; Beitinger & Fitzpatrick 1979; Matthews & Hill 1979) and can have primacy in influencing habitat choice over other factors such as food availability. For instance, when temperature and food were both varied, water temperature, as measured through behavioral thermoregulation, was a better predictor of Bluegill habitat selection than were predictions based on optimal foraging or behavioral energetics (Wildhaber & Crowder 1990). This led the authors to suggest that habitat decisions based on temperature and food abundance were processed hierarchically by Bluegills (i.e., temperature first and then food level) rather than being integrated. In particularly harsh habitats, high temperatures have a major influence on habitat use by fishes. In a combination of field and laboratory tests, the Red Shiner strongly avoided near-lethal temperatures (e.g., 37°C) that occurred in the main channel of the Canadian River, Oklahoma, in late summer (Matthews & Hill 1979) as did other common minnow species in the system (WJM unpubl. data). During extremes of summer heating, all fish species were scarce in the exposed mid-channel (hot water over a shallow sand-bed substratum) and were crowded into a limited part of the habitat in slightly deeper pools at the river edge where riparian trees provided shade (Matthews & Hill 1980).

Effect of Habitat Size on Fish Assemblages

The positive relationship between habitat area or volume and species richness is well documented for a wide range of habitats and organisms including fishes (e.g., lakes: Barbour & Brown 1974; Jackson & Harvey 1989; Amarasinghe & Welcomme 2002; streams: Gorman & Karr 1978; Swift et al. 1986; Sheldon 1987; Osborne & Wiley 1992; Taylor 1997; Matthews 1998) (Fig. 1.12). Even so, we know less about what factors actually result in the relationship and might be responsible for variations in the pattern (Connor & McCoy 1979; Angermeier & Schlosser 1989). In a comparison of small streams in Minnesota, Illinois, and Panama, species richness in pools and riffles generally was correlated better with habitat volume than area, and richness also was related to the total number of individuals and to habitat complexity. In general, the strongest predictor of species richness was the number of individuals, followed by habitat volume and habitat complexity (Angermeier & Schlosser 1989). These data suggest that the general relationship between species richness and habitat size is primarily a sampling phenomenon because larger habitats contain more individuals and thus tend to better sample the regional faunas (see Connor & McCoy 1979) and is due less to increased complexity in larger areas or to a balance between immigration and extinction rates (see MacArthur & Wilson 1967). Because the number of individuals was not related consistently to habitat volume, as would be expected if species-area relationships were strictly caused by sampling more individuals, Angermeier & Schlosser (1989) concluded that the relationship

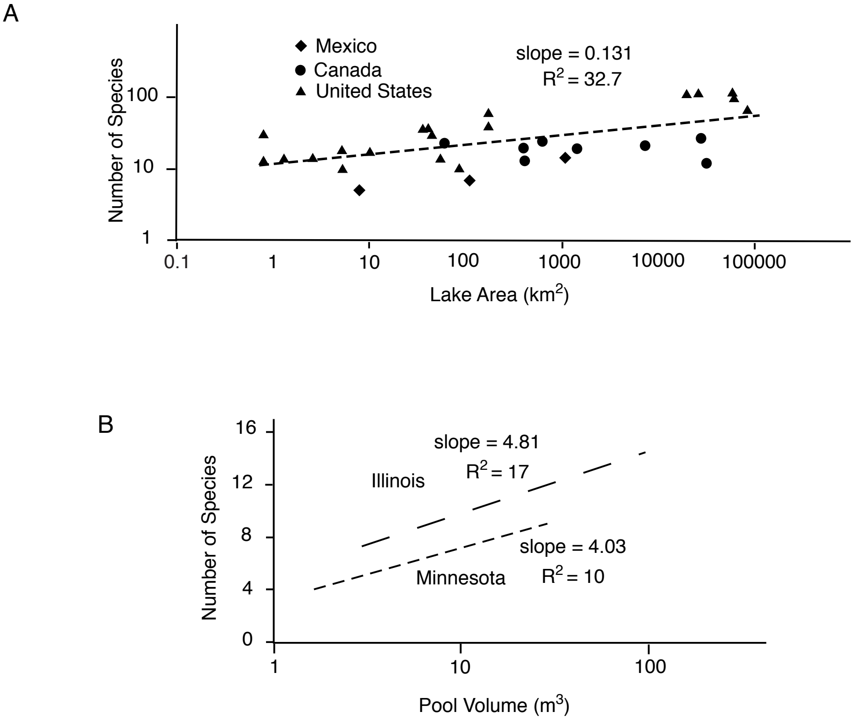

Figure 1.12. The effect of habitat area or volume on the number of fish species in: (A) North American lakes (based on data from Barbour & Brown 1974; dashed line shows least square regression) and (B) streams in Illinois and Minnesota (based on data from Angermeier & Schlosser 1989).

is driven by multiple factors, including aspects of immigration-extinction and habitat diversity in addition to passive sampling.

The relationship of the species-area phenomenon to the regional influence on species diversity is also important. Although an increase in species richness with area or volume of habitat is pervasive among different assemblages, much of the variation in the strength of this relationship likely has to do with regional effects, such that streams or lakes of similar size cannot be expected to support the same number of species without consideration of the region that they occupy. This is illustrated by comparing species-rich eastern U.S. streams with species-poor western streams of the same size. A further illustration of this is given by the species richness patterns of tributary streams in upper and lower portions of river drainages. Tributary streams entering the main channel low in the system (adventitious streams, Gorman 1986) support more species than tributary streams of the same approximate size that enter the main channel high in the system (Fausch et al. 1984; Osborne & Wiley 1992; Thomas & Hayes 2006; Roberts & Hitt 2010).

Formation of Assemblages

The question of how species are added to existing assemblages (assuming that the habitat is suitable) and whether there are any rules that govern the order and kind of species additions has intrigued ecologists for decades. With the increasing rate of introduction of non-native species, the question has taken on broader concern in attempting to develop models predicting the vulnerability of native communities to invasion by non-native taxa. The resolution of the question could be approached at a larger scale to include both historical (i.e., lineage) and dispersal components, although much of the ecological literature has focused on a finer scale that emphasizes dispersal (but see Gorman 1992; Winston 1995).

A seminal paper by Diamond (1975) on addition of bird species to islands initiated a debate that continues in some measure to the present. He hypothesized that species comprising a community are selected and co-adjusted in their niches and abundances, so that they fit with each other and resist invaders. Later studies focused on testing observed patterns against null models of species assembly (e.g., Connor & Simberloff 1979), resulting in the demonstration that at least some of the patterns used to invoke assembly rules could be attributed to chance. The use of null models increased the rigor of studies on assembly rules, although philosophical differences in constructing the null model continue to foster debate (Jackson et al. 1992; Gotelli & Graves 1996; J. H. Brown et al. 2000; Stone et al. 2000; Fox 2001).

Gorman (1992) analyzed assemblage formation in several Ozark upland streams and argued that general patterns of habitat use and ecological interactions were ancient evolutionarily and not the result of an ongoing, contemporary process. Consequently, the occurrence of fish species on a macrogeographic level (i.e., drainage) was best predicted by historical, biogeographic factors, but contemporary ecological processes best predicted abundance patterns in local assemblages.

A meta-analysis of 96 published studies of species presence-absence matrices, comprising a wide range of taxa and geographic locations, was used to determine the generality of Diamond's (1975) model of assembly rules (Gotelli & McCabe 2002). Most plant and animal assemblages followed predictions of Diamond's assembly rules in that fewer species combinations occurred than expected by chance, a result also shown by community assembly studies using laboratory microecosystems (Drake et al. 1993). Although fish assemblages in the meta-analysis evidenced less structuring by competition, the low sample size ($n = 3$) precluded meaningful generalities. The efficacy of Diamond's assembly rules for freshwater fishes was tested for phoxinin cyprinids inhabiting streams of the Red River drainage, Texas, Oklahoma, and Arkansas (Winston 1995). Species pairs that were most similar morphologically co-occurred significantly less often than expected by chance. Because the co-occurrence of species that were most closely related did not differ from random, interspecific competition was deemed the most likely mechanism causing the pattern (Winston 1995).

A study on small headwater streams in eastern Oklahoma also indicated that interactions among fish species could impact the structure of benthic fish assemblages so that observed species-area relationships resulted in fewer species than predicted by null models (Taylor 1996). Interactions of two species, the Banded Sculpin and Orangethroat Darter, were studied using manipulative field experiments and demonstrated that asymmetrical interference competition was responsible in part for the difference between observed and expected species densities. The Banded Sculpin caused a shift in habitat use of the Orangethroat Darter but not the reverse (Taylor 1996). Analysis of 249 Canadian lakes from 5 different regions within the Laurentian Great Lakes area also demonstrated that fishes had a nonrandom spatial distribution. The most likely reason was common use of particular habitats and impacts of predation rather than competition (Jackson et al. 1992). Overall, evidence is convincing that fish assemblages are highly structured; suggested mechanisms include competition, physical habitat selection, and predation. As a caveat, however, studies addressing factors governing the formation of fish assemblages are still rare.

Are species characteristics such as body size, geographic range, and population sizes related to the ability of species to colonize habitats? Based on a long-term study of fishes in the Cimarron River by the late Jimmie Pigg, colonization potential of fish species was, not surprisingly, correlated with species' abundance, but geographic range size and body size were not (Gotelli & Taylor 1999). A similar relationship of high colonization and low extinction probabilities being correlated with mean population size, but not with body size or trophic position, was found for upland fishes in the Ouachita Highlands (Taylor & Warren 2001). Other studies suggest that the strongest determinant of colonization potential is the match between species tolerances and the physical habitat. For instance, Moyle & Light (1996ab) developed a set of empirically based predictions regarding colonization success in fishes. Although the predictions were developed largely to understand invasions of non-native species, most are also applicable to colonization potential of native species with the caveat that they were developed for western (California) fish assemblages. A principal conclusion of their work was that the primary factor in the success of an invading fish species was the match between the invader and the hydrologic regime. Even so, the ability of a species to match the requirements of the physical habitat may be necessary but not sufficient for a particular species to invade a given habitat. In Brier Creek, and other nearby tributaries to the large Lake Texoma reservoir on the Texas-Oklahoma border, the formerly abundant Red Shiner (*Cyprinella lutrensis*) disappeared or became extremely scarce since the 1980s, likely due to a complex interplay of changes in stream morphology and increases in predation pressure in the creeks (Matthews & Marsh-Matthews 2007). Following a massive flood of the reservoir and these tributaries in 2007, Red Shiners reappeared in at least two of the streams but did not persist or expand in numbers. There were no apparent changes in physicochemical conditions like temperature in these creeks, thus the species was presumed to still match the physical environment but was held in check, as shown experimentally, by Sunfish predation (Marsh-Matthews et al. 2011).

Another key point, also supported by a study of North American freshwater drainages (Gido & Brown 1999), is that all aquatic systems are invasible. Numerous authors (e.g., Ross 1991; Lodge 1993) have suggested that species-rich assemblages, like those of the southeastern United States, were more resistant to invasion by non-natives when compared with species-poor systems. Given the fact that these are rich systems and that these systems have gained native species richness both by in situ speciation and colonization, it stands to reason that species with appropriate physiological tolerances and ecological characteristics can enter and become established in species-rich assemblages. In addition, although depauperate native fish faunas tend to have more invasive species, the difference is essentially an artifact of the pool of potential non-native fishes being greater for systems with low native fish diversity (Gido & Brown 1999).

A model to predict invasion success of six fish species (including natives and non-natives) to a western Sierra, cool-water (trout zone) stream incorporated life history responses to biotic factors of competition and predation and the physical factor of stream discharge (Strange & Foin 2001). Predictions of the model were tested against a data set of relative abundance of fishes for Martis Creek from 1979 to 1994 and Sagehen Creek from 1952 to 1961. Model predictions generally captured major trends in species' relative abundances for Martis Creek and showed good fit to data for Sagehen Creek, especially for the Brown Trout, Tahoe Sucker (*Catostomus tahoensis*), and Paiute Sculpin (*Cottus beldingii*) (Fig. 1.13). Key points from this six-species system are that invasion sequence, competition, and predation were all important, but the relative importance of these factors varied based on hydrological conditions. In particular, the sequence of floods and droughts had a major impact on the relative abundance and potential for invasion of each species. The role of invasion sequence or priority effects (e.g., Morin 1987) has been examined rarely in the formation of fish assemblages. Strange & Foin (2001) incorporated the role of variability of physical factors and illustrated how this changes biotic responses. Hence, their key point is that assembly from the same species pool probably will result in alternate or multiple states as the physical regime changes rates of biotic processes.

PERSISTENCE OF FISH ASSEMBLAGES IN SPACE AND TIME

We have considered formation and variation of fish assemblages over evolutionary time scales and how faunal

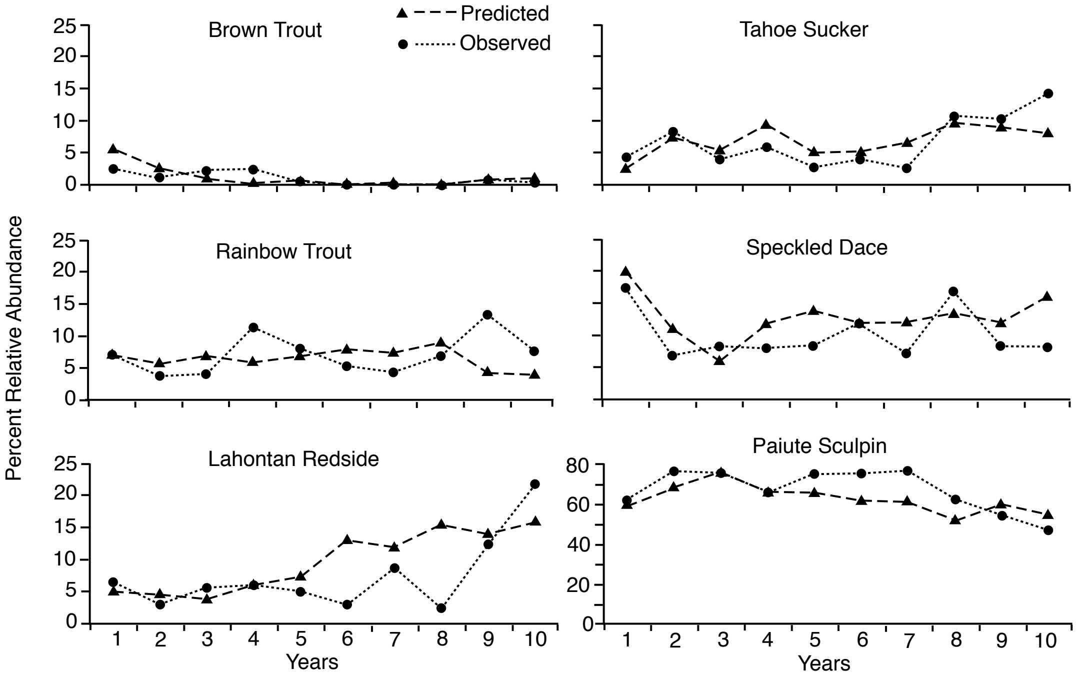

Figure 1.13. Model predictions compared with actual relative abundance data from Sagehen Creek, California (data from Strange & Foin 2001). Note the change in y-axis scale for the Paiute Sculpin, *Cottus beldingii.*

changes occur over large geographic spatial scales. Of interest now is how persistent fish assemblages are over ecological time scales and over more localized spatial scales. In part because of different approaches to the problem and different ecological scales, conflicting views prevail on the stability, persistence, or lack thereof, in fish populations (Rahel et al. 1984; Yant et al. 1984; Matthews et al. 1988; Grossman et al. 1990; Matthews 1998; Berra & Petry 2006). For instance, statistical measures based on comparisons of presence-absence (a measure of assemblage persistence), ranks in abundance (a measure of assemblage change), and variation in actual or relative numbers (a measure of change among individual species as a part of the total assemblage; Grossman et al. 1990) form a transformation series reflecting increased sensitivity to change. That numbers of individuals of a given species show the greatest variation is not surprising, given that most long-term studies of fish assemblages use sampling techniques that are not designed to provide rigorous estimates of absolute or total population size (Matthews 1998). Thus, not only the analytical scale, as illustrated above, but also the temporal and spatial scales of the analysis have strong effects on the outcome. As suggested by Rahel (1990), studies addressing stability and persistence of assemblages should investigate multiple levels within the hierarchical framework. Separating actual changes in species presence or absence from artifacts of sampling also is a pervasive and significant problem (Magnuson et al. 1994). We also suggest that the goal of research in this area should not be to determine whether local assemblages did or did not change because the suggestion that local fish assemblages do not change would be illogical—all local assemblages change as individuals are added or removed (due to natality and mortality, or movements). Instead, as data sets become longer (e.g., several to many samples over a period of years to decades) it becomes of more interest to ask how much a local fish assemblage, or distribution of fish species within a watershed, has changed during various intervals. In particular, ecologists are increasingly interested in contrasting the observed changes in local fish assemblages during intervals with major events (like serious droughts or floods) with the changes that occur during intervals lacking such disturbance factors. Put another way, are the changes that can be observed in fish assemblages over long periods of time related more to gradual changes or to dramatic events that may (or may not) leave their mark for years or more?

Understanding the stability and persistence of fish assemblages is important for several reasons (e.g., Grossman et al. 1990; Matthews 1998). First, assessment of the impact of human-caused environmental change requires an understanding of natural variation in assemblages. Second, the degree to which assemblages show stability, persistence, or both, over space and time relates to inferred control mechanisms operative within the assemblage. In general, aquatic assemblages showing little persistence or stability are thought to be governed primarily by random (stochastic; non-equilibrial) processes (e.g., floods, droughts, disease outbreaks) in contrast to assemblages showing high persistence or stability, which are thought to be controlled primarily by structured (niche-related; deterministic) processes (e.g., competition and predation) (Moyle & Vondracek 1985; Matthews 1998). Many ecological models dealing with competition, predation, and population growth assume stable age distributions, an assumption that would not be met if assemblages were inherently unstable (Grossman et al. 1982).

Changes in both numbers and kinds of fish species in a habitat can be mediated by natural variation in physical factors (e.g., temperature, drought, flooding, water quality), biotic factors (e.g., competition, predation, facilitation), or human impacts via habitat modification or the introduction of non-native species. In addition, fish assemblages might vary over time in the apparent absence of major changes in their habitat. For instance, 7 replicated small fish assemblages, identical in terms of species numbers and kinds, were stocked in semi-natural, outdoor artificial streams and studied over a period of 388 days (Matthews & Marsh-Matthews 2006a). Even though the streams were as identical as possible, differences developed in the extent of algal cover and the level of predation with the latter caused by the differential survival of Sunfish among pools. Consequently, even in the absence of natural disturbances, the assemblages diverged significantly in composition so that the ultimate structure of any of the experimental assemblages was not predictable from its initial structure, suggesting that these systems were not controlled by strong equilibrial processes (Matthews & Marsh-Matthews 2006a).

Another important aspect of persistence of community structure derives from the fact that fish species of all kinds can have important effects on the ecosystem, ranging from top-down or cascading trophic effects (Power et al. 1985, 2008; Power 1990) to direct effects on ecosystem processes (e.g., Gelwick & Matthews 1992) to a wide range of indirect effects in ecosystems (Flecker et al. 2010; Gido et al. 2010b). To make matters more complicated, the effects of any particular species or groups of species in an ecosystem may be strongly related to the history of recent disturbance (e.g., flood or drought) with different functional groups of fishes exerting differential effects on emergent ecosystem properties throughout the time course of recovery from the disturbance (Gido et al. 2010). To the extent that the role of each species can be predicted, it follows that knowing the likelihood of change in its abundance can enhance predictions of changes in ecosystem properties in some future climate.

Longstanding questions about the role of invasive species include the degree that native fish faunas are directly harmed by the influx of extralimital species so that native species decline as hardier invaders increase, often in conjunction with habitat degradation, or that changes in native fish faunas relate primarily to natural or anthropogenic changes in fundamental properties like stream flow. In a recent test of this question for European streams on the Iberian Peninsula, the abundance of invasive species was a better predictor of declines in native fish species than was habitat degradation (Hermoso et al. 2011). In contrast, in tributaries to the upper Gila River, New Mexico, changes in abundance of several native species were related more over a 21-year period to variation in discharge than to densities of non-native predators (Stefferud et al. 2011).

Physico-chemical Responses

As evidenced by the preceding sections, fishes respond to physical aspects of their environment including droughts, floods, temperature, dissolved oxygen, and pH. Based on an analysis of 25 long-term (≥2 years; median 11 years; range 2–45 years) studies of lotic systems, 76% showed high persistence and 52% showed high stability in at least one type of analysis (Table 1.2). The studies were designed or amenable to testing assemblage persistence and stability and included 3 to 95 species. Increasing environmental harshness, especially if the harshness was related to anthropogenic impacts, resulted in decreases in persistence and stability. In systems judged to have low stress, all were persistent and 80% were stable. In contrast, in systems judged to have moderate or high stress, only 22% were persistent and 11% stable. For systems with obvious human disturbance, only 14% were considered persistent or stable (Table 1.2). The degree of stability in assemblages also varies depending on the metric used to test it. Measures based on numbers of individuals indicate much greater variation, even in streams judged to be benign.

Some fish assemblages in geographic regions prone to extreme climatic conditions do show persistence in the face of such environmental challenges. These faunas have been under strong, long-term selection to deal with such conditions, and intolerant species were extirpated (e.g., Smith & Powell 1971). For example, the fish assemblages in Brier Creek, Oklahoma, are routinely subjected to floods and droughts (Table 1.2) (Ross et al. 1985; Matthews

Table 1.2. Long-term (≥2 years) studies of North American stream fish assemblages organized by benign versus harsh environments (modified from Matthews 1998). Relative stream size is based on stream orders when available (small stream orders 1–3; medium stream orders 4–6; large river orders >6); latitude and longitude are from about the midpoint of the study area; spatial scale, if not stated, was estimated from map of study area. Spp. = Number of species analyzed; HD = Human disturbance; L = Low stress; P = Persistence; S = Stability; C_j = Jaccard Coefficient; PSI = Proportional Similarity Index; CV = Coefficient of Variation (proportion); I_m = Morisita's index of similarity.

Site	Habitat	Stations	Potential Stressor and Categorization of Stress	Spp. (no.)	Authors' Conclusions	HD	L	High P	High S	References
Ball Creek, NC	Small stream	1	Spring flooding; late spring to autumn drought (generally low stress)	3	Temporal persistence of resident species; moderate temporal stability of resident species based on numbers of individuals (mean CV = 0.53)	N	Y	Y	Y	Freeman et al. (1988)
Ball Creek, NC	Small stream	1	Spring flooding; late spring to autumn drought (generally low stress)	4	Temporal persistence of resident species; temporal stability of resident species based on relative abundance; moderate to low temporal stability based on numbers of individuals (mean CV = 0.75)	N	Y	Y	Y	Freeman et al. (1988)
Coweeta Creek, NC	Medium stream	1	Spring flooding; late spring to autumn drought (generally low stress)	5	Temporal persistence of resident species; temporal stability of resident species based on relative abundance; moderate to low temporal stability based on numbers of individuals (mean CV = 0.62)	N	Y	Y	Y	Freeman et al. (1988)
Cedar Fork Creek, OH	Medium stream	1	Annual flooding (moderate stress)	30	Temporal persistence; temporal stability indicated by consistency in rank order data; high variation in numbers of individuals	N	Y	Y	Y	Meffe & Berra (1988)
Undisturbed streams, Savannah River site, SC	Small stream	9	Annual variation in flow (low stress)	15[a]	Temporal persistence overall; temporal stability based on rank order data and similarity analyses; moderate stability based on CV of 0.44	N	Y	Y	Y	Paller (2002)
Martis Creek, CA	Small stream	4	Periodic flooding; non-native predators (moderate stress)	7	Temporal persistence overall; temporal stability based on rank order data; number and biomass data showed high variation (last sample in 1983)	N	Y	Y	Y	Moyle & Vondracek (1985)

Black Creek, MS	Medium stream	5	Annual overbank flooding (low stress)	25	Temporal persistence; temporal stability based on numbers of individuals and rank order data	N	Y	Y	Y	Ross et al. (1987)
Piney Creek, AR	Medium stream	5	Periodic flooding (low stress)	10	Temporal persistence overall; temporal stability overall based on rank order data and similarity analyses; temporal stability at individual stations based on rank order data	N	Y	Y	Y	Ross et al. (1985); Matthews et al. (1988)
Pearl River, MS	Large river	8	Periodic flooding; upstream impoundments (generally low stress)	28	Temporal persistence overall; temporal stability overall based on similarity analyses; high variation in numbers of individuals (CV = 1.03)	N	Y	Y	Y	Gunning & Suttkus (1991); data analyzed by Matthews (1998)
French Creek, NY	Small to medium stream	9	Normal seasonal variation in flow and temperature (low stress)	41	Temporal persistence overall; temporal stability based on species abundances	N	Y	Y	Y	Hansen & Ramm (1994)
Kiamichi River, OK	Medium stream	6	Annual high flows (low stress)	10	Temporal persistence of common species overall; temporal stability overall based on rank order data and similarity analyses; stability at three individual stations and instability at three others based on rank order data	N	Y	Y	Y	Matthews et al. (1988)
Coweeta Creek, NC	Medium stream	1	Annual variation in flow, including droughts (generally low stress)	16	Temporal persistence of common species (mean $C_j = 0.79$; range 0.67–1.0); temporal stability altered by drought (pre-drought, drought, and post-drought assemblages distinct)	N	Y	Y	N	Grossman et al. (1998); additional analysis by STR
Otter Creek, IN	Medium stream	1	Upstream mill dam; no other major impacts (low stress)	18	Temporal persistence (mean $C_j = 0.80$); low to moderate stability (PSI = 0.47); low stability based on numbers of individuals (CV = 1.37)	N	Y	Y	N	Whitaker (1976); Grossman et al. (1982); data reanalyzed by Matthews (1998)
Martis Creek, CA	Small stream	4	Periodic flooding; severe spring flood in 1983; non-native predators (generally low stress)	5	Temporal persistence overall; low temporal stability based on relative abundance data (species abundances changed dramatically after 1983 flood)	N	Y	Y	N	Strange et al. (1992)

(continued)

Table 1.2, continued

Site	Habitat	Stations	Potential Stressor and Categorization of Stress	Spp. (no.)	Authors' Conclusions	HD	L	High P	High S	References
Sagehen Creek, CA	Small stream	11	Periodic flooding; severe winters; no major human disturbances (low to moderate stress)	8	Temporal persistence; moderate temporal stability based on rank order data; low temporal stability based on changes in standing crop	N	Y	Y	N	Gard & Flittner (1974)
Aravaipa Creek, AZ	Medium stream	3	Flash flooding and drought (moderate to high stress)	7	Temporal persistence of species overall; temporal stability based on rank order data; actual numbers fluctuated extensively	N	N	Y	Y	Meffe & Minckley (1987)
Brier Creek, OK	Small stream	5	Flash flooding and drought (moderate to high stress)	10	Temporal persistence overall; low temporal stability overall based on rank order data and similarity analysis ($I_m = 0.40$)	N	N	Y	N	Ross et al. 1985; Matthews et al. (1988)
Purgatoire River tributaries, CO	Small streams; some intermittent	5	Flash flooding and drought (high stress)	11	Temporal persistence at four of five sites (fifth site had intermittent flow); low temporal and spatial stability due primarily to variation in numbers of rare species; stability greater in sites with deep pools than with only shallow riffles	N	N	Y	N	Fausch & Bramblett (1991)
Wabash River, IN	Large river	29	Dam construction; positive and negative changes in water quality; urbanization; periodic flooding (moderate stress)	75	Moderate temporal persistence overall; low temporal stability overall based on Bray-Curtis similarity; similarity decreased with greater time between samples to about 0.25; low similarity at individual stations based on multivariate measures using abundances	Y	N	Y	N	Pyron et al. (2006)

Blue River, KS	Large river	14	Reservoir construction; introduction of non-native species (moderate stress)	29	Low to moderate persistence (mean $C_j = 0.41$; range 0.2–0.54) temporal stability based on relative abundances	Y	N	N	Y	Gido et al. (2002)
Disturbed streams, Savannah River site, SC	Small stream	8	Post-thermal discharge; periodic anoxic discharge; toxic chemicals (high stress)	14[a]	Low temporal persistence; low temporal stability overall based on rank order data and similarity analyses; mean CV = 0.59, based on numbers of individuals	Y	N	N	N	Paller (2002)
Little Uchee Creek, AL	Small stream	2	Increase in pine monoculture; 69% human population increase in region; 39% decline in annual flow; flashier runoff (moderate stress)	12	Low to moderate temporal persistence with rare species eliminated (mean $C_j = 0.57$; range 0.22–1.0); moderate temporal stability (mean $I_m = 0.71$; range 0.22–0.96)	Y	N	N	N	Johnston & Maceina (2009); additional analysis by STR
Halawakee Creek, AL	Small stream	2	Increase in pine monoculture; 69% human population increase in region; flashier runoff (moderate stress)	15	Low temporal persistence with rare species eliminated (mean $C_j = 0.33$; range 0.22–0.40); low temporal stability (mean $I_m = 0.53$; range 0.36–0.71)	Y	N	N	N	Johnston & Maceina (2009); additional analysis by STR
Wacoochee Creek, AL	Small stream	4	Increase in pine monoculture; 69% human population increase in region; flashier runoff (moderate stress)	20	Low to moderate temporal persistence with rare species eliminated (mean $C_j = 0.27$; range 0.14–0.50); low temporal stability (mean $I_m = 0.53$; range 0.24–0.88)	Y	N	N	N	Johnston & Maceina (2009); additional analysis by STR
Bogue Chitto River, LA	Medium stream	7	Land-use changes including increases in human population, dairy farming, cattle ranching, gravel mining, road construction, and silviculture (moderate stress)	95	Low to moderate temporal persistence ($C_j = 66–74\%$); temporal stability low (27-year comparison) to high (11- and 16-year comparisons)	Y	N	N	N	Stewart et al. (2005); additional analysis by STR

[a] Average over all sites.

et al. 1988). In spite of extreme conditions, including total dewatering of some stream reaches, the fish fauna over an 18-year period showed strong persistence on a streamwide basis with abundant species remaining abundant and rare species remaining rare with only a few exceptions (Table 1.2). Stability (a quantitative measure) of the Brier Creek fish fauna showed greater variation, and the fauna at individual collection sites (i.e., at the assemblage level) was even less persistent and stable.

Long-term stability (or changes) in a fish community in arid or semi-arid environments may depend substantially on the response of individual species to drought conditions. Experiments on five common fish species in Brier Creek showed species-specific responses to drought with respect to outright survival and to post-drought recovery. For example, the Blackstripe Topminnow (*Fundulus notatus*) and Longear Sunfish (*Lepomis megalotis*) had lower survival during simulated drought compared to Central Stonerollers, Bigeye Shiners (*Notropis boops*), and Orangethroat Darters. Orangethroat Darters that survived an experimentally imposed drought in one summer actually recovered in physical condition to match that of conspecifics in the wild and were reproductively competent (Marsh-Matthews & Matthews 2010). Importantly, in systems with strong environmental filters, assemblages may be controlled more by stochastic processes, even though the high persistence of species might suggest primacy of niche-related processes (Chase 2007).

Long-term data also exist for Piney Creek, a permanent upland Ozark stream (Ross et al. 1985; Matthews 1986c; Matthews et al. 1988) that offers a more benign habitat (i.e., no dewatering and less temperature variation). Not surprisingly, Piney Creek fishes also were highly persistent; however, in contrast to Brier Creek, the fish fauna in Piney Creek also had greater faunal stability, both overall and at the assemblage level. Piney Creek had a severe flood in December 1982; however, immediately after the flood no major changes occurred in rank abundance of the 10 most abundant species (Matthews 1986c). Less common species did change in abundance so that local assemblages were altered immediately post-flood. Eight months after the flood, the overall fish fauna and the fauna at individual collecting stations had essentially recovered to pre-flood conditions, rendering the Piney Creek fish fauna stable and persistent across years and a range of flow conditions (Matthews 1986c).

Although fish assemblages clearly can rebound rather quickly from major impacts (see also Detenbeck et al. 1992 and Taylor et al. 1996a), other studies indicate that floods or droughts changed or reset assemblage structure. Later studies on Brier Creek documented that two severe droughts resulted in a substantial change in the Brier Creek fauna, which did not recover to its former state until 3–4 years post-drought (Matthews & Marsh-Matthews unpubl. data). In Coweeta Creek, North Carolina (Table 1.2), a severe drought resulted in 3 distinct assemblages over a 10-year period corresponding to pre-drought, drought, and post-drought (Grossman & Ratajczak 1998; Grossman et al. 1998). Finally, in a 22-year study of a 150 km reach of the Pearl River, Louisiana and Mississippi, fish assemblages showed stochastic structuring resulting from droughts, hurricanes, dams, and channel modifications. Even so, in periods between major perturbations, biotic interactions were likely important in structuring assemblages (Geheber & Piller 2012).

Much of the detected variation in persistence and stability of fish assemblages is perhaps related to hydrologic variability, the variation from system to system in what composes a catastrophic event, and the timing of major perturbations (Grossman & Sabo 2010). Flooding in Brier Creek when fishes are spawning can have severe impacts on larval survival, as shown when a major flood displaced downstream and killed larval cyprinids and centrarchids <10 mm TL (Harvey 1987). In contrast to the December flood in Piney Creek, a second flood of similar magnitude in March–April 2008 had much more lasting effects. Even after 2 years the community had not converged back to its normal condition (WJM pers. obs.).

Likewise, a severe spring flood in Martis Creek (Table 1.2) changed assemblage composition from the domination of native, spring-spawning species to domination by the non-native, autumn-spawning Brown Trout (Strange et al. 1992). In a northwestern fish assemblage in the John Day River drainage, Oregon, fishes that spawned in late spring and summer, such as the Speckled Dace and Bridgelip Sucker (*Catostomus columbianus*), incurred high losses of young-of-the-year individuals to summer flooding, but early spring spawners, such as the Rainbow Trout, were more susceptible to spring flooding when the developing embryos were still in the redds (gravel nests) (Pearsons et al. 1992). Losses of fishes from flooding were greater in stream sections with low habitat complexity, suggesting that complex habitats may act as sources of individuals for the colonization of structurally simple habitats (Pearsons et al. 1992).

Relatively few studies are available with suitable data for assessing temporal persistence and stability of fish assemblages in lakes and reservoirs (Table 1.3). In our analysis of 9 long-term studies (median duration 15 years; range

Table 1.3. Long-term (≥2 years) studies of North American lake and reservoir fish assemblages organized by benign versus harsh environments (NL=natural lake; R=reservoir; na=not available). Latitude and longitude are from the approximate midpoint of the study area; Spp.=Number of species analyzed; HD=Human disturbance; L=Low stress; P=Persistence; S=Stability; C_j=Jaccard Coefficient; CV=Coefficient of Variation.

Site	Habitat	Temporal Scale (years)	Potential Stressor and Categorization of Stress	Spp. (no.)	Authors' Conclusions	HD	L	High P	High S	References
Little Nauyuk Lake, NW Territory, Canada	NL	15	Initial heavy fishing exploitation followed by cessation of exploitation (low)	1	Temporal persistence; temporal stability based on age structure	Y	Y	Y	Y	Johnson (1994)
Gavia Lake, NW Territory, Canada	NL	15	Light to moderate fishing exploitation followed by cessation of exploitation (low)	1	Temporal persistence; temporal stability based on age structure	Y	Y	Y	Y	Johnson (1994)
Small Wisconsin lakes (7)	NL	11	Natural variation (generally low)	1–22	Moderate temporal persistence (species turnover 0–1.1% per year)	N	Y	Y	na	Magnuson et al. (1994)
Lake Texoma	R	43	Natural and human-caused variation in inflow; summer hypoxia; turbid inflows; introduction of non-native fishes (moderate)	11	Temporal persistence; temporal stability based on rank order data and similarity analyses; moderate stability based on numbers of individuals (mean CV=0.58)	Y	N	Y	Y	Gido et al. (2000)
Lake Michigan	NL	12	Commercial fishing; fish stocking; introduction of non-native species (high)	18	Temporal persistence; low temporal stability based on changes in relative abundance, fishery landings, and catch-per-unit effort	Y	N	Y	N	Eck & Wells (1987)
Lake Mendota, WI	NL	72	Shoreline urbanization; introduction of non-native aquatic plants (moderate to high)	20	Low temporal persistence (eight species extirpated); low temporal stability based on relative abundance	Y	N	N	N	Lyons (1989)
Wintergreen Lake, MI	NL	15	High nutrient inflow; loss of native predator due to winterkills in 2 years followed by reintroduction of native predator (high)	8	Moderate temporal persistence (two species extirpated by winterkill); low temporal stability based on pre- and post-winterkill assemblages and pre- and post-predator introduction assemblages; high temporal stability based on recovery to initial conditions following native predator reintroduction	Y	N	N	N	Mittelbach et al. (1995)
Chequamegon Bay, Lake Superior; shallow water	NL	24	Changes in water quality; introduction of non-native species (moderate)	12	Temporal persistence (mean C_j=0.80); temporal stability based on multivariate analyses of abundances	Y	N	Y	Y	Hoff & Bronte (1999)
Chequamegon Bay, Lake Superior; deep water	NL	24	Changes in water quality; introduction of non-native species (moderate)	8	Temporal persistence (mean C_j=0.83); low temporal stability overall (three distinct assemblages over time)	Y	N	Y	N	Hoff & Bronte (1999)

11–72 years) of lentic fish assemblages (8 natural lakes and 1 impoundment), the levels of persistence and stability were essentially the same as those for lotic systems. Reduced persistence or stability of assemblages tends to occur in altered habitats or in habitats impacted by non-native plants or animals. In contrast to lotic systems, all but one of the lentic studies had suffered moderate or major human impacts, primarily through commercial fishing pressure, the introduction of non-native plants and animals, and overall urbanization within the watershed.

Johnson (1994) examined long-term faunal stability in two small Arctic lakes over a 15-year period. Only the Arctic Charr (*Salvelinus alpinus*) was studied, but it was the sole species in one lake and one of two species in the other. After an initial period of moderate (one lake) and high (the other lake) fishing exploitation, the lakes were allowed to recover for several years. In both, age and size structure of Arctic Charr returned to the original condition, indicating population stability. In six small Michigan lakes, changes in the fish assemblages were generally low over a 4-year period, as determined from a measure of community heterogeneity (based on the average percent dissimilarity over all possible pairs of seine sites within lakes) (Benson & Magnuson 1992). Somewhat surprisingly, heterogeneity among seine hauls within a site (33 m of shoreline) was of the same magnitude as heterogeneity among sites, thus suggesting that fishes responded to small-scale patchiness of the environment. A pelagic reservoir fish assemblage was persistent and stable over a 43-year period, based on the rank order of species, except for the introduction of 2 species within the study period, the Striped Bass and Threadfin Shad (*Dorosoma petenense*) (Gido et al. 2000). The numbers of individuals fluctuated greatly with coefficients of variation of the 11 species across years ranging from 11 to 108%.

In general, lentic systems showing less persistence or stability tend to be those with altered habitat or with non-native plants, fishes, or other organisms. For example, Lake Michigan has received considerable study because of heavy fishing pressure and the introduction of non-native species such as the Sea Lamprey (*Petromyzon marinus*), Alewife (*Alosa pseudoharengus*), Rainbow Smelt (*Osmerus mordax*), Coho Salmon (*Oncorhynchus kisutch*), Chinook Salmon (*O. tshawytscha*), Rainbow Trout, Brown Trout, and Brook Trout (*Salvelinus fontinalis*). Many native species, such as the Lake Trout (*Salvelinus namaycush*), Bloater (*Coregonus hoyi*), and Lake Herring (*C. artedii*), have declined substantially or increased as numbers of non-native fishes have fluctuated. Although biological interactions like competition may be important (e.g., Stewart et al. 1981), the major reason for the changes in abundance may be predation on early life history stages (Eck & Wells 1987). A similar pattern of decline in native species following introduction of non-native fishes and bivalves has occurred for deep-water fish assemblages in Lake Huron (Riley et al. 2008). Major shifts in species composition of a small Michigan lake also happened after loss and then reintroduction of the Largemouth Bass (see predation subsection) (Mittelbach et al. 1995).

Finally, two syntheses project substantial changes in species distributions under future climate scenarios and thus composition of local assemblages in lakes and streams. A review and synthesis of projected responses of fishes in shallow lakes to global climate change suggested the likelihood of massive changes, including widespread local extinctions, changes in assemblage composition with encroachment of warm-water species into previously cold lakes, changes in competitive relationships, reduced species richness, and more variable abundances in lakes of the future (Jeppesen et al. 2010). Similarly, a projection of future distributions of 35 fish species across 1,110 stream sites in France (Buisson et al. 2010) predicted a decrease in distribution of some cold-water species (e.g., Brown Trout), but widespread increases in occurrence of many cool-water or warm-water species that might colonize newly suitable sites.

The stability of fish assemblages when faced with physico-chemical change may be achieved through resistance, the ability of the populations to withstand the disturbance, or by adjustment stability, the ability of the populations to recover quickly following a disturbance (Connell & Sousa 1983; Ross et al. 1985). Resistance includes enhanced physiological tolerance to environmental perturbations or well-developed refuge-seeking behavior. Elasticity, a component of adjustment stability, may occur through high rates of population increase following a disturbance or through rapid movement back into the affected area from refuges (Ross et al. 1985). Both may be important, depending on the nature of the habitat (Matthews 1986c; Fausch & Bramblett 1991). Cutthroat Trout populations in a high-gradient Oregon stream showed resilience in recovering from a catastrophic debris flow in ≤3 years. Recovery was initially from immigration into the disturbed area followed in the second and third years by enhanced recruitment (Lamberti et al. 1991). Recovery of a southeastern fish assemblage following dewatering of stream sections required 6–7 months and initially occurred through immigration followed by reproduction

(Adams & Warren 2005). A 9-year study of recolonization of a South Carolina river after a diesel oil spill showed that strong similarity between recovery and control sites was not reached until 52 months post-disturbance. Sites in the river closest to unimpacted reaches recovered most rapidly because they were closest to a source pool for reinvasion of fishes into the local sites (Kubach et al. 2011).

It is especially important to consider long-term faunal shifts in streams that experience changes in climate or other natural conditions in addition to marked anthropogenic impacts. Continuous sampling for 23 years in a small European stream showed that modifying the stream to remove riparian vegetation and straighten the channel caused pervasive changes in the fish community, more so than long-term changes in the local climate with no return to former conditions of the community (Penczak 2011). A 24-year evaluation of fish assemblages in the Wabash River, Indiana, showed a change from fishes that prefer upstream habitats (e.g., cobble substrate, faster currents, with little silt) to groups more typical of slow waters and with greater silt tolerance (Beugly & Pyron 2010). These changes coincided with increases in siltation in the river that effectively altered the entire ecosystem. Particularly where anthropogenic impacts are involved, it seems obvious that one additional major factor is the specific nature of the disturbance (e.g., acute toxicity, persistence of the toxicity, physical habitat modification), and each such event likely is unique with recovery depending on site-specific factors. In some cases long-term loss of species may have occurred within some groups that was not attributable to any one specific anthropogenic factor. For example, a general loss of darter (Percidae) species occurred in streams of northeastern Oklahoma over a span of half a century, apparently related to anthropogenic changes in the region (e.g., dam construction), but the loss could not be attributed to any single, clearly identifiable human-related factor (Gillette et al. 2012). Directional (away from original condition) changes in plains fish assemblages in the central United States is strongly related to changes in flow regime, which is related to human modification of the landscape, particularly water-use facilities and overall increases in human population pressure (Taylor 2010).

So, at the scale of the entire assemblage, persistence is fairly common and stability somewhat less so, although both can be impacted by the timing and magnitude of perturbations. Much less is known about the persistence and stability of particular species associations within an assemblage. Detecting patterns in species associations of mobile animals is challenging because the scale of observation is such that individuals found in the same sample have a high probability of having been in close contact with each other in nature. As a result, one might assume direct interactions among individuals. Most survey methods for fishes, or other mobile vertebrates, actually have fuzzy boundaries, and finding two species in a sample may not equate to their direct interaction. In addition, fishes found together in a relatively long reach of stream (e.g., Matthews & Marsh-Matthews 2006b) may, especially in highly structured habitats, occupy different pools or riffles and thus not encounter each other on a daily basis.

For mobile animals distributed across a heterogeneous landscape, consistent spatial associations among species could exist because some species (or some life stages within a species) select similar microhabitats (Chapman & Chapman 1993; Grossman et al. 1998; Wilson 1999) independent of each other. The persistence of direct contacts of 8 taxonomic species (minnows, a Topminnow, Sunfishes, and black basses) and 11 ecospecies (with the Sunfishes separated into piscivorous adults versus insectivorous juveniles) were assessed by snorkel surveys across 14 adjacent pools within 1 km of Brier Creek at various intervals over a period of 22 years (Matthews & Marsh-Matthews 2006b). Associations among multispecies groups were concordant across slightly more than half of the total of 18 different intervals between surveys. For the 2 years with the most within-year surveys, associations of species were concordant within the year. Across years, associations of species were concordant in late summer, but not in spring or in autumn. Associations typically were not changed by events like floods and droughts, but the second of two severe droughts in 3 years coincided with distinct changes in associations of species or ecospecies. The empirical evidence suggests that although some smaller species groups (pairs, triads, or foursomes) were consistently in direct contact across years or even decades, little evidence emerged that whole assemblage, multispecies associations were constant or that selection pressures due to such multispecies groups would be consistent across such periods of time.

INTERACTIONS WITHIN FISH ASSEMBLAGES

To anyone who has spent time watching fishes in nature, a wide range of interactions among individuals and species is obvious. Interactions may be intense, such as intraspecific behaviors associated with spawning or strong compensatory responses in foraging to the presence of a predator or competitor, or interactions may seem essentially nonexistent. Direct contacts among species have strong implications for fish assemblage structure in both ecological and evolutionary time because behaviors of one species, like foraging, microhabitat use, or reproduction, can be modified by contact with other species. As emphasized by Thompson (1988:81), the challenge in the study of interspecific interactions is to understand "the origins and partitioning of variation in outcomes of interactions between species."

Studies of fish resource partitioning (i.e., how coexisting species differ in resource use) show that species in an assemblage often segregate on the basis of food kind or size, subtle differences in habitat use, or the times they are active (Ross 1986). The mechanisms behind the differences in resource use are less understood. Before the 1980s, the tendency was to interpret such differences more as a direct response to contemporary rather than historical interactions, even though information from systematics was used to select closely related taxa that might best show compensatory responses (Brooks & McLennan 1991). The rise of phylogenetic systematics in the 1970s, coupled with changes in the understanding of adaptation (Gould & Lewontin 1979) and a much more critical approach to studies of natural selection (Rose & Lauder 1996), set the stage for a new approach to the understanding of ecological differentiation of organisms. Works by Brooks (1985), Mayden (1987a), and Brooks & McLennan (1991) demonstrated that ecological or life history traits might be better explained by lineage characteristics than by contemporary interactions in an assemblage. If the ecological trait in question is also present in other species in an organism's lineage, then there is no reason to invoke ongoing competition or recent evolution within the species to explain it. Today, the interpretation of differences in resource use among species is moving toward a balance between historical effects and ongoing interactions among individuals and species. As outlined by others (Mayden 1987a; Brooks & McLennan 1991), if good phylogenies exist for the taxa in question and if ecological characters are described for all terminal groups in the analysis, objective methods exist for determining whether ecological traits are plesiomorphic (i.e., ancestral traits) or apomorphic (i.e., derived traits) and perhaps due to ongoing species interactions.

Within an assemblage of species, fishes may interact through competition, predation, facilitation, or mutualism, and such interactions may affect the ultimate composition of an assemblage (Fig. 1.2). With fishes, as with other taxa (e.g., Boucher et al. 1982; Stachowicz 2001; Bruno et al. 2003; Hay et al. 2004), competition and predation have received the most attention by far, but the positive interactions of facilitation and mutualism are much less studied.

Given that individuals of a species begin feeding as larvae when only a few millimeters long and, depending on the species, may grow to many centimeters or even meters, interactions among fishes and other organisms in their community may shift between predation, competition, or some form of facilitation or mutualism. The direction of the interaction also may change as a function of growth (Werner & Gilliam 1984; Polis et al. 1989). The ontogenetic impact on competition and predation clearly increases the complexity of interactions in fish assemblages so that outcomes are difficult to predict. For example, Fast et al. (1982) documented growth responses of Bluegills and Largemouth Bass following the colonization of a southern California reservoir in 1958 by Threadfin Shad. Although Threadfin Shad are eaten by Largemouth Bass and other centrarchids, the impact of their introduction on growth of Largemouth Bass was varied. Age-1 Largemouth Bass and Bluegills, which feed primarily on small prey such as zooplankton (Ross 2001), showed decreased growth following the introduction of Threadfin Shad. This was interpreted as being caused by competition for food with the planktivorous Threadfin Shad (Fast et al. 1982). In contrast, age-2 Largemouth Bass, which were large enough to prey on Threadfin Shad, showed increased growth rates, and age-2 Bluegills (which do not prey on Threadfin Shad and which likely shifted in resource use so that there was less food overlap with that species) did not respond to Threadfin Shad.

Competition

Studies of competition in fish assemblages have been addressed through observational field studies (which cannot prove the existence of competitive interactions, but can show the potential for competition if large overlaps occur in resource use and if resources are limiting), so-called natural experiments, manipulative field or laboratory experiments, and various combinations of these approaches. As an example of an observational study, eight common cyprinid species in a southeastern U.S. blackwater stream differed in microhabitat use (Baker & Ross 1981; Fig. 1.14) with four pairs segregating primarily in water-column position, followed by separation within each pair primarily on the basis of association with aquatic vegetation. The one exception was the benthic pair, the Longnose Shiner (*Notropis longirostris*) and Longjaw Minnow (*Ericymba amplamala* as Silverjaw Minnow, *Ericymba buccata*, Pera & Armbruster 2006; Schönhuth & Mayden 2010), which were essentially identical in measured habitat parameters but which differed in active feeding times (Longjaw Minnow primarily at night, Longnose Shiner primarily during the day). Vertical segregation of fishes also occurred in a study of a nine-species fish assemblage within a 37 m section of an Appalachian stream (Grossman & Freeman 1987). The species (all in different genera) segregated into a water-column guild (five species) and a benthic guild (four species). Guilds were stable seasonally and annually, and guild members apparently did not differ in habitat use. The differences in microhabitat use between guilds were attributed to common selective pressures or to phylogenetic constraints on the species and not to ongoing biotic interactions with the possible exceptions of the Warpaint Shiner and Rosyside Dace (*Clinostomus funduloides*) (Grossman & Freeman 1987). In a later paper, individual-based optimal foraging models better explained habitat differences between these two species than did interspecific interactions (e.g., Grossman et al. 2002). Observational field studies addressing interactive segregation among fishes continued to be prevalent in the ecological literature through the 1980s and mid-1990s. Of 37 papers reviewed by Matthews (1998) that dealt with habitat or food segregation of North American freshwater fishes, 32 (86%) found evidence of segregation and 14 (44%) of these studies inferred that competition was involved.

Gorman (1992) also examined vertical segregation of a suite of minnow species in two streams of the Ozark Highlands (Fig. 1.6) and one in northern Illinois, in the Wisconsin Driftless region, an area not covered by the Wisconsinan glacial advance. He combined laboratory studies of habitat preferences and interactive habitat use with historical data from phylogenetic relationships of the minnows and an area cladogram showing relationships of the streams the minnows inhabited (Fig. 1.15). Four species (Central Stoneroller; Largescale Stoneroller, *Campostoma oligolepis*; Hornyhead Chub, *Nocomis biguttatus*; and Ozark Minnow, *Notropis nubilus*) occurred in all three streams under consideration and, based on the area cladogram, were considered part of the ancestral fauna. All of these species were bottom or near bottom inhabitants that shifted little in vertical water-column position in the presence of other species. Species occupying middle and upper regions of the water column were more recent additions to the fauna. In addition, these species showed greater evidence of interspecific interactions, suggesting that niche partitioning involving mid-pelagic species had not yet reached an evolutionary equilibrium. The near absence of the Bigeye Shiner (*Notropis boops*) in the North Fork was perhaps due to its replacement by the Telescope Shiner (*Notropis telescopus*), another large-eyed pelagic minnow (Gorman 1992). Resolution of this question would require knowing if the Bigeye Shiner occurred in the drainage before the arrival of the Telescope Shiner. In contrast to purely observational studies, studies such as Gorman's (1992) allow a fuller understanding of the differences in resource use among co-existing species.

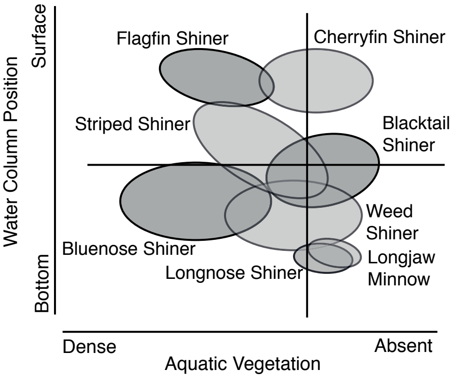

Figure 1.14. Observed resource segregation among cyprinids in Black Creek, Mississippi. Data show 75% confidence ellipses along discriminant function I (water-column position) and II (amount of aquatic vegetation) (modified from Baker & Ross 1981).

A problem with observational studies is the usual lack of a clear null hypothesis from which to judge observed differences among co-habiting taxa in such things as resource use. In non-experimental research, data are collected and evaluated for their consistency with specific hypotheses or with the operation of a specific causal process, but without the knowledge of what values might be attributed to similar data in the absence of these causal processes. Consequently, a non-null hypothesis often is used as the tested hypothesis. Null models ideally should be used as a first step in evaluating non-experimental evidence (Connor & Simberloff 1986). A null model generates the distribution of values for the variable of interest in the absence of a putative causal process (e.g., how probable could the observed values occur simply by chance?). Null models are not without their own problems, especially because the way a null model is

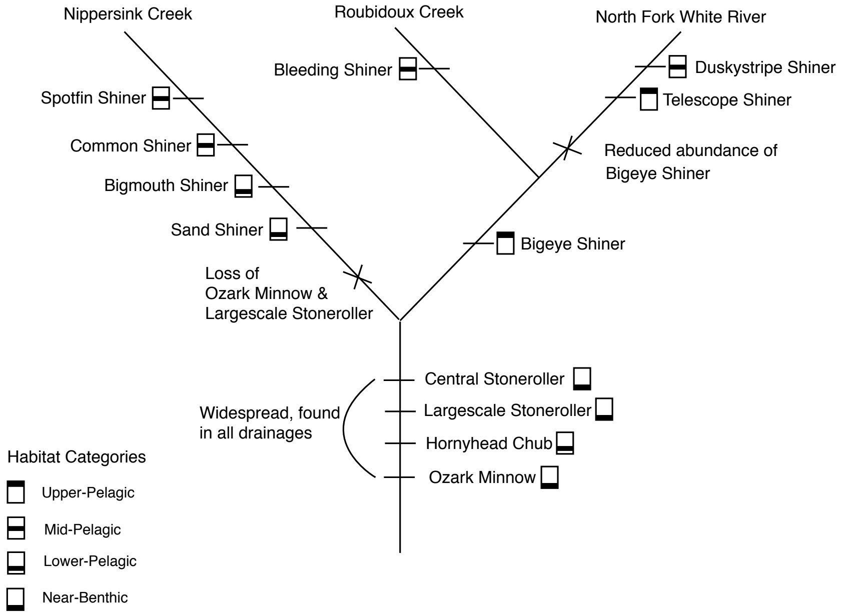
Nippersink Creek
Roubidoux Creek
North Fork White River
Bleeding Shiner
Duskystripe Shiner
Spotfin Shiner
Telescope Shiner
Common Shiner
Reduced abundance of Bigeye Shiner
Bigmouth Shiner
Sand Shiner
Bigeye Shiner
Loss of Ozark Minnow & Largescale Stoneroller
Central Stoneroller
Widespread, found in all drainages
Largescale Stoneroller
Hornyhead Chub
Ozark Minnow
Habitat Categories
Upper-Pelagic
Mid-Pelagic
Lower-Pelagic
Near-Benthic

Figure 1.15. An area cladogram of three streams showing predominant minnow species (Cyprinidae, Carps and Minnows) overlain with their water-column positions. See text for further explanation (modified with permission from Gorman 1992; copyright Leland Stanford University).

constructed can control the outcome, and a profuse literature has formed around this issue (see review by Gotelli & Graves 1996).

Natural experiments are offered in situations where a species occurs in different combinations with other species; however, such studies may suffer from a lack of suitable controls, as well as other problems. Nonetheless, such studies can provide compelling evidence of competition. Douglas et al. (1994) studied habitat use (niche shifts) of a southwestern minnow, the Spikedace (*Meda fulgida*), in the presence and absence of an introduced minnow, the Red Shiner (*Cyprinella lutrensis* as *Notropis lutrensis*). In allopatry, both species occupied similar habitats that were significantly shallower and with slower current and finer substrata compared with overall habitat availability. In syntopy, Red Shiner habitat use did not change from allopatric use, but Spikedace were displaced into swifter current.

Studies of character displacement and release take an approach similar to that of natural experiments but with an evolutionary rather than ecological time scale. Ecological character displacement involves disruptive selection and phenotypic divergence, presumably in response to competitive interactions, in sympatric species (Schluter & McPhail 1992; Schluter 2000; Pfennig & Pfennig 2009). Ecological character release involves a shift in characters in allopatric compared with sympatric populations (Robinson & Wilson 1994). Both displacement and release often invoke competition as the driving force so that the distinction between the two is simply the historical pattern of events (Robinson & Wilson 1994). In their review of fishes (emphasizing lake species) and ecological character displacement and release, Robinson & Wilson (1994) concluded that competition is often a driving force in lacustrine systems as evidenced from frequent examples of character displacement and release. Further, the changes often include shifts between benthic and limnetic forms. Examples of ecological character displacement involving benthic and limnetic forms are particularly well demonstrated among populations of Threespine Sticklebacks (*Gasterosteus aculeatus* complex, Gasterosteidae) and Sunfishes (*Lepomis* spp., Centrarchidae) and tend to occur in species-poor, relatively young environments (Robinson et al. 2000; Bolnick & Lau 2008).

At least six lakes in southwestern British Columbia, along the Strait of Georgia, have species pairs of the Threespine Stickleback complex with one member of a pair primarily benthic and the other limnetic (Schluter & McPhail 1992; Rundle et al. 2000; Baker et al. 2005). In these, as in other Stickleback populations in North America, colonization of freshwater habitats was by the marine, anadromous form over the last 12,000–20,000 years as the Cordilleran ice sheet began to retreat from northwestern North America (Bell & Foster 1994; Clague & James 2002; Bell et al. 2004). Mitochondrial DNA analysis indicates that neither limnetic nor benthic types form a single lineage among lakes. Instead, relationships of species pairs are closer within lakes, indicating that species pairs apparently evolved independently on a lake-by-lake basis from the ancestral, anadromous stock (Taylor & McPhail 1999; Wund et al. 2008). Benthic forms tend to be larger bodied and to have fewer and shorter gill rakers, wider gapes, and greater body depth compared with limnetic forms (Schluter & McPhail 1992). Resource use follows form with limnetic forms obtaining most prey from the plankton, except during the breeding season when males establish nests and attract females in the littoral zone of lakes. In lakes with single species, resource use tends to be more generalized over benthic and planktonic habitats. Overall, the results strongly suggest that the divergence of benthic and limnetic forms occurred via resource competition, a finding supported experimentally (Schluter 1994; Bolnick 2004).

A similar pattern of benthic and limnetic forms is apparent with *Lepomis* spp. (Sunfishes). In the Adirondack region of the northeastern United States, Bluegills and Pumpkinseeds often occur together in lakes with Bluegills occupying the water column and feeding primarily on planktonic prey, and Pumpkinseeds occupying the benthic, littoral zone and feeding mostly on benthic invertebrates (Robinson et al. 1993, 2000). In lakes without Bluegills, Pumpkinseeds also may have a planktonic form that occurs in the water column and feeds primarily on planktonic prey such as cladocerans. Morphological divergence between the open- and shallow-water forms varies among lakes but is generally well developed (Robinson et al. 2000). Morphologically, the planktonic form of Pumpkinseed tends to approach the morphology of typical Bluegills with shallower, longer bodies and longer pectoral fins. Further, the more extreme limnetic forms of Pumpkinseed have faster growth rates and better condition than fish with intermediate body forms (Robinson et al. 1996). These lakes likely have been without Bluegills since they were formed as Pleistocene glaciers withdrew some 17,000 years ago (Dyke et al. 2002). The most likely explanation for the development of the planktonic form of Pumpkinseed is the exploitation of planktonic prey made available by the absence of Bluegills (Robinson et al. 1993), although diffuse competition from other planktivorous fishes also can reduce the extent of morphological divergence (Robinson et al. 2000).

Although well-designed field experiments also can have problems (see Hurlbert 1984; Eberhardt & Thomas 1991), they often are considered the best evidence for competition in nature (see reviews by Schoener 1983; Connell 1983). An early experiment of this sort was the manipulation of ponds to test for competition among three species of *Lepomis* (Bluegill; Green Sunfish, *Lepomis cyanellus*; and Pumpkinseed) (Werner & Hall 1976). Habitat use and growth rates were monitored for fishes held in allopatry and in syntopy. Release from interspecific competition was evidenced by the increased growth in isolation with Bluegills showing the greatest release. In allopatry, all three species obtained ≥40% (dry weight) of their diets from vegetated habitats. In syntopy, Green Sunfish continued to feed in vegetation, but Bluegills shifted primarily to open water and Pumpkinseeds shifted to benthic prey. Later, for Bluegills and Pumpkinseeds, Mittelbach (1988) tested the hypothesis that the predator avoidance movement of juvenile Bluegills from open water to vegetation resulted in competition among small fishes in the vegetation refuge. Cages arrayed along the vegetated littoral zone of a lake were stocked with two juvenile Pumpkinseeds and varying numbers of Bluegills. The growth of both species declined linearly in response to increased fish density in the cages, indicating that the concentration of small fishes in the vegetated littoral zone can lead to competition for food. In addition, increases in fish density resulted in decreases in invertebrate body length and decreases in the density of large invertebrate prey in the cages. Further, the density of large invertebrates was related positively to growth rates of both sunfish species. The mode of competition was most likely exploitative (passive), although Mittelbach (1988) could not rule out the possibility of interference (active) competition.

Specific habitats occupied by individual fish also may be affected by competitive interactions, including both interference and exploitation (see Begon et al. 1996; see previous subsection on formation of assemblages, e.g., asymmetrical interference competition between the Banded Sculpin and Orangethroat Darter, Taylor 1996). Competitive interactions within a non-native salmonid assemblage (Brook Trout, Brown Trout, and Coho Salmon) were measured in a laboratory stream (Fausch & White 1986). In syntopy, Coho Salmon could defend profitable foraging sites against Brook Trout and Brown Trout, and Brook Trout, in contrast to field observations, could displace Brown Trout from profitable sites. Under allotopic conditions, both trout species increased their breadth of foraging sites, including those sites with the highest profitability. Shifts in habitat use under syntopy were due to aggressive behavior of the dominant fish, thus making this an example of active competition. The interaction of the introduced Rainbow Trout and the native Rosyside Dace was investigated by underwater observations in pools of a North Carolina stream (Freeman & Grossman 1992). Rosyside Dace spent less time in feeding areas and had lower feeding rates when Rainbow Trout were present compared with when they were absent. The Rainbow Trout were too small to act as predators and rarely were overtly aggressive toward the dace. The presence of Rainbow Trout apparently lessened the value of a particular feeding site for Rosyside Dace (Freeman & Grossman 1992), making this an example of exploitative competition. The interaction was asymmetrical because Rosyside Dace apparently did not impact habitat selection by Rainbow Trout (Grossman & Boulé 1991). In fact, asymmetry is the general rule among competitive interactions (Schoener 1983).

Intraspecific interactions also can impact the structure of fish assemblages (Fausch & White 1986; Freeman & Stouder 1989; Matthews 1998). For example, Red Shiners held at densities from about 3 to 30 individuals/m^2 in large experimental streams had moderately reduced overwinter survival that was negatively related to initial stocking density, and density had a strong, linear effect on growth the following spring (Matthews et al. 2001). At high population densities, growth was highly skewed with fewer individuals growing large enough to reach sexual maturity. In a subsequent experiment (WJM unpubl. data), Red Shiners with free access to a series of pools and riffles in predator-free experimental streams typically formed groups with densities lower than those that had resulted in low modal growth in the groups in the previous experiment (Matthews et al. 2001). This finding suggests that fish may avoid excessively dense aggregations (unless factors like predators or differences in habitat quality provide stronger stimuli). In a combined observational and experimental study of foraging patch selection and use by Mottled Sculpins in two streams in the Coweeta Creek watershed, North Carolina, adult Mottled Sculpins established feeding territories in patches that had greater prey densities and prey renewal rates in contrast to randomly selected patches or patches occupied by juvenile Mottled Sculpins. Adult fish also abandoned patches when prey levels dropped with larger adult fish giving up the patches sooner (at higher prey densities) compared with smaller adult fish. Intraspecific competition is indicated because feeding patches chosen by adult fish were rapidly occupied by juveniles if the adults were removed (Petty & Grossman 2010).

As exemplified above, competitive interactions among or within species can affect fish assemblages on both ecological and evolutionary time scales. On ecological time scales, competition can result in changes in resource use, changes in growth rates and condition, and presumed changes in fitness. On evolutionary time scales, competitive interactions can provide strong selective forces resulting in genetically fixed differences in morphology and behavior, leading, at least in some cases, to speciation. Unequivocal evidence of competitive exclusion of one species by another, other than in laboratory experiments, is difficult to obtain and is uncommon for any taxonomic group (Ricklefs 1990; Begon et al. 1996), including North American native fishes. In fact, various studies suggest that physical variation in flow and temperature, recolonization dynamics, and temporal variation in reproduction have greater impacts on North American fish assemblages than competitive exclusion (Schlosser 1982; Grossman & Freeman 1987; Grossman & Boulé 1991).

A study of the Dolly Varden (*Salvelinus malma*) and Cutthroat Trout involving field observations, laboratory experiments, large-scale 28-year field manipulations using whole-lake transplants, and physiological studies of retinal structure related to visual acuity (reviewed by Northcote 1995; Jonsson et al. 2008) did not demonstrate competitive exclusion, although interactive interspecific segregation was indicated. Experimentally, allopatric Dolly Varden showed greater shifts in habitat use than Cutthroat Trout, indicating that the former may be more affected by interspecific competition. Northcote (1995) concluded that many of the apparent exclusions that are observed in temperate natural populations of closely related species pairs may be the temporary (geologically speaking) product of pioneer species invading habitats available after deglaciation and exploiting those habitats and conditions where previous selection provided those species with long-term competitive advantages.

Loss of species due to competition may be more prevalent in terms of impacts of non-native species on native species (reviewed by Fausch 1988; Ross 1991; Fuller et al. 1999). For instance, in the Pecos River, the native Rio Grande Silvery Minnow (*Hybognathus amarus*) was replaced by the introduced Plains Minnow (*Hybognathus placitus*) over about a 10-year period. The most likely hypothesis for the exclusion is competition, given that hybridization did not seem to be a factor. Both species use similar habitats and have equivalent life histories (Moyer et al. 2005). Even for the relatively well-studied cases of interactions of native and introduced salmonids, clear evidence of the mechanism involved where interactive segregation in habitat use was demonstrated is generally lacking (Fausch 1988). Where mechanisms of interaction are documented, impacts of direct predation are better supported than competition (Ross 1991).

Predation

Impacts of predation on fish assemblages include changes in species composition, shifts in resource use, alteration of life history patterns, moderation of competitive interactions, and reduction of survivorship of various age classes. These effects can substantially alter both the kinds of species and the sizes of individuals occurring in a local fish assemblage (Fig. 1.2).

Alteration of species composition is perhaps the most obvious impact of predators and tends to occur in species-poor systems. Examples include small, glacier-formed lakes in Alberta, Canada, which have fish faunas of two main types: those dominated by large predators (Northern Pike, *Esox lucius*, and Yellow Perch) and generally lacking small-bodied species, and those dominated by small-bodied forms such as the Brook Stickleback (*Culaea inconstans*) and Fathead Minnow (*Pimephales promelas*) (Robinson & Tonn 1989). A similar pattern occurs in small, glaciated lakes in Wisconsin, where the two dominant assemblage types were centrarchid–Northern Pike lakes and lakes dominated by the Central Mudminnow (*Umbra limi*) and cyprinids (Tonn & Magnuson 1982). The centrarchid–Northern Pike assemblage only occurred in lakes with high winter oxygen levels; the absence of the Central Mudminnow–cyprinid assemblage from such lakes was likely due to predation. The loss of species because of non-native predator impacts has occurred in species-poor southwestern U.S. streams. For example, widespread declines and extirpations have occurred throughout the native range of the Gila Topminnow (*Poeciliopsis occidentalis*), most likely related to habitat loss and the introduction of non-native predators, including Western Mosquitofish (Meffe et al. 1983). Experimentally, non-native Western Mosquitofish (*Gambusia affinis*) can eliminate the native livebearer by predation on young individuals (Meffe 1985). Similarly, in the Colorado River system, adults of the introduced Red Shiner prey on larval Colorado Pikeminnow and may be an important factor in the decline of this large, piscivorous minnow (Bestgen et al. 2006). In the lower Yakima River, Oregon, the introduction of non-native Smallmouth Bass has altered the size-based predation risk on native salmonids. The Northern Pikeminnow (*Ptychocheilus oregonensis*), which is now rare, did not consume large numbers of salmonids until it exceeded 250 mm FL; in contrast, Smallmouth Bass ≤250 mm FL consume more salmonids than larger bass. Because of the size dynamics, predation risk has been reduced for larger prey (spring Chinook Salmon, Coho Salmon, and steelhead), but increased for the smaller, ocean-type Chinook Salmon (Fritts & Pearsons 2006).

A common impact of predation is a spatial or temporal shift in habitat use. Terrestrial and aquatic piscivores differ in the size-selective distribution of predation risk so that large fishes have greater risk in shallow water from avian and mammalian predators and thus shift to deep water. In contrast, small fishes have greater risk in deep water from aquatic predators and thus reduce risk by moving to shallow habitats (Power 1987; Gelwick 1990; Harvey & Stewart 1991; Schlosser 1991). The interactions of predation risk, habitat depth, and fish size were modeled for North American stream fishes (see Schlosser 1991; Harvey & Stewart 1991, based on Power 1987). We suggest that the model should also apply to lentic systems to illustrate the roles that size-selective predation, species differences in body size, and ontogenetic changes in size have in affecting habitat selection (Fig. 1.16). In shallow water, large fishes are at their greatest risk from wading mammals and birds. In deep water, small fishes (with the exception of small fishes such as larvae) are at their greatest risk from piscivorous fishes.

Fishes, and other animals (Lima & Dill 1990), balance the risk of predation against the rewards from foraging (e.g., Werner et al. 1983b; Gilliam & Fraser 1987; Werner & Hall 1988). Also, as energy stores are depleted, either through starvation or through the effects of parasite loads, fishes tend toward more risk (e.g., Giles 1987). In a replicated experiment in a small stream, predation contributed to the strong positive relationship between fish size and habitat depth (Harvey & Stewart 1991). Survival decreased for large individuals of the Central Stoneroller, Creek

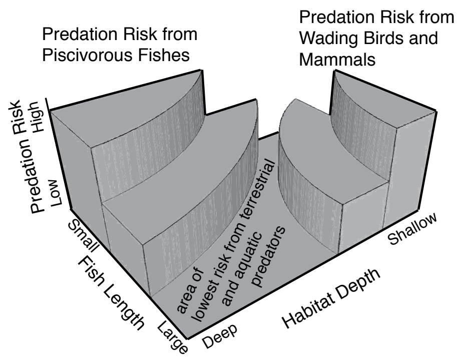
Predation Risk from Piscivorous Fishes
Predation Risk from Wading Birds and Mammals
Predation Risk
High
Low
Small
Fish Length
Large
area of lowest risk from terrestrial and aquatic predators
Deep
Habitat Depth
Shallow

Figure 1.16. A model of the interaction of water depth and the risk of size-specific predation from birds and mammals (shallow water, large prey) and piscivorous fishes (deep water, small prey) (based on Power 1987, Schlosser 1991, and Harvey & Stewart 1991).

Chub, and Striped Shiner (*Luxilus chrysocephalus*) in shallow versus deep habitats with low survival in shallow habitats attributed to predation by terrestrial predators (e.g., herons and raccoons). The threat of predation from aquatic predators also results in a shift of small fishes into shallow, often vegetated, habitats, even though growth rates generally could be optimized by moving to deeper water (Power et al. 1985; Post & McQueen 1988; Werner & Hall 1988; Angermeier 1992).

In a series of studies in small northern lakes and experimental ponds on the ontogenetic shifts in habitat by Bluegills in response to Largemouth Bass predation, changes in habitat use resulted from a tradeoff between rates of growth and risks of predation (Werner et al. 1983b; Werner & Hall 1988). In ponds with predators, young Bluegills spent several years in vegetated, littoral habitats before venturing into the more energetically profitable, but riskier, pelagic zone with the switch in habitat occurring between 51 and 83 mm SL. Variation in body size and age of the habitat shift was a function of the density of Largemouth Bass and thus the degree of predation risk. Depending on survivorship of Largemouth Bass age cohorts, in most cases by the time Bluegills reached 60–100 mm SL their risk of predation by Largemouth Bass dropped substantially. Consequently, Bluegills could assess the relative degrees of habitat profitability and risk of predation and balance their choice of habitat accordingly. The decision to avoid the more profitable but riskier areas is not without its own costs because growth in Bluegills restricted to the less profitable vegetated habitats was 27% less than control fish in a profitable and predator-free habitat.

The costs of predator avoidance, in this case cannibalism, on growth and survival also was shown in a replicated, whole-lake experiment using different age groups of Rainbow Trout. In the absence of large Rainbow Trout, age-0 trout used all habitats (littoral and pelagic), but they tended to be restricted to the less profitable littoral zone when large Rainbow Trout were present. Young Rainbow Trout were trading off rapid growth in the more food-rich pelagic zone against the greater predation risk found in that zone. The cost included lower growth rates for age-0 trout restricted to the littoral zone, which showed an almost 50% reduction in September body mass compared with the same-age trout in lakes without predators (Biro et al. 2003).

Substantial evidence exists showing that piscivorous Largemouth Bass or Spotted Bass (*Micropterus punctulatus*) can exert strong, top-down trophic effects through at least two levels in small stream ecosystems, resulting in substantial shifts in assemblage structure. Among pools in Brier Creek, Oklahoma, a strong negative association existed in the distribution of large (>100 mm TL) individuals of the two bass species and the Central Stoneroller (Power & Matthews 1983). In pools with schools of the Central Stoneroller, attached algae (mostly *Rhizoclonium* and *Spirogyra*) was much reduced in height and standing crop from grazing by these algivorous fish. In contrast, Central Stoneroller was absent or rare in pools containing large bass, and these pools had dense, tall growths of algae. This pattern, once detected, was tested across time and by bass addition-removal experiments (Power et al. 1985) and persisted throughout a year of study. The addition of Largemouth Bass to a predator-free pool containing Central Stonerollers resulted in a major change in composition and growth form of algae in the pool. Once Largemouth Bass were introduced, Central Stonerollers rapidly emigrated out of the test pools (Power et al. 1985; Power 1987) or took shelter and remained in shallow pool edges. As a result, algae grew densely over the next several weeks in the deeper parts of the pools guarded by bass, and algal growth gradually spread into shallow areas as the numbers of Central Stonerollers decreased through emigration. This was interpreted as an example of a three-level trophic cascade with strong effects by the bass controlling ecosystem processes in these pools. The effects of the algivorous Central Stoneroller in stream ecosystems are pervasive. By removal of algae they initiate changes within pools with consequences for invertebrates, processing of particulate organic matter, and bacterial standing crops, causing a total of >20 measurable ecosystem responses (Matthews et al. 1987; Gelwick & Matthews 1992; Matthews 1998).

In Brier Creek, the reciprocal distribution of large bass and Central Stoneroller is temporally persistent. In six of eight surveys (Power et al. 1985; Matthews et al. 1994), the dichotomy in pool-to-pool distribution persisted across 14 pools for >1 year, and 12 additional surveys (1995–2003) indicated the pattern was again persistent (Matthews & Marsh-Matthews 2006b). In addition, these piscivores also result in avoidance of pools by some, but not all, other small-bodied and potential prey species and thus have major effects on local assemblage structure.

Across streams, the impacts of bass species on prey fishes, particularly cyprinids, are variable and depend strongly on the physical setting of a stream and identity of the potential predator. When a search for the existence of the bass-stoneroller-algae trophic cascade was extended to other, larger stream systems, where Smallmouth Bass were the dominant predator, the dichotomy between bass and stonerollers broke down, and they often were found together in pools (Matthews et al. 1987). Smallmouth Bass apparently were a less controlling predator than the other bass species, and this was confirmed when Smallmouth Bass were moved to an experiment in Brier Creek (Harvey et al. 1988). In seeming contrast, two size classes of another cyprinid, the Hornyhead Chub, reduced their use of deep pools of an experimental stream in the presence of Smallmouth Bass and instead occupied shallow raceways, suggesting the importance of particular species or systems in affecting the strength of the predation response (Schlosser 1988b).

In many systems (Matthews 1998) top-down predation or predator threat by piscivores can control one or more lower trophic levels in a classic HSS (Hairston-Slobodkin-Smith) pattern (Slobodkin et al. 1967). It is equally clear from the above examples that few patterns fit widely across all systems and all potential predators, and each situation probably needs to be assessed for its own unique properties when we consider effects of piscivores on species occurrences in local assemblages and on food webs.

The family Cyprinidae (Carps and Minnows), although composed primarily of small-bodied species, also includes taxa that are large-bodied and piscivorous, such as *Ptychocheilus* spp., the pikeminnows (140–180 cm TL) (Page & Burr 1991), and Creek Chub (maximum size about 300 mm TL, Ross 2001). Following the introduction of the non-native Sacramento Pikeminnow (*Ptychocheilus grandis*) in the Eel River, California, habitat use of native fishes shifted (Brown & Moyle 1991). Responses of native fishes generally followed the predictions of the body size, predation risk, and water depth model (Fig. 1.16). Resident fishes shifted from broad use of riverine habitats to general avoidance of deep habitats, either by shifting microhabitat use within a habitat or by shifting habitats. Changes were most extreme for the Threespine Stickleback, juvenile Sacramento Sucker (*Catostomus occidentalis*), and juvenile Rainbow Trout, which shifted to habitats that were shallower than the shallowest depth usually occupied by Sacramento Pikeminnow (about 50–70 cm deep).

Creek Chubs become increasingly piscivorous at >80 mm SL (Fraser & Cerri 1982), and large Creek Chubs can impact smaller fishes, including juvenile Creek Chubs (e.g., Fraser & Cerri 1982; Fraser & Emmons 1984; Schlosser & Ebel 1989). Even in small streams with distinct pool-riffle habitats, the impact of Creek Chubs on habitat use of juvenile conspecifics or small cyprinid species, although measurable, is less extreme than that shown by prey fishes in the presence of bass species (Fraser & Cerri 1982; Schlosser & Ebel 1989). In a replicated, experimental stream, juvenile Creek Chubs and Blacknose Dace were less numerous in treatment compartments containing adult Creek Chubs than in those without the predator (Fraser & Cerri 1982; Fraser & Emmons 1984). Responses of the prey to the predator also were mediated by time of day and habitat structure with both reducing the effect of the predator. The prey selected habitats with cover and a predator over those that lacked cover and a predator, and prey were more likely to be associated with a predator during the day than at night, when predation risk was presumably greater. Prey responses to the predator varied depending on the amount of food available to the prey. Juvenile Creek Chubs accepted greater predation risk as the potential reward (greater food density) increased (Gilliam & Fraser 1987). Later work in a natural stream (Fraser et al. 1987) generally supported the results from the experimental stream, except that predator avoidance by the prey did not vary with the amount of habitat structure (probably because there was always some structure in the natural stream) nor diurnally.

An exception to the rule of small fishes in shallow habitats and large fishes in deep habitats can occur with larval fishes. In both lentic (e.g., Werner & Hall 1988) and lotic (e.g., Harvey 1991ab) systems, large predators can create predator-free zones for larval fishes by eliminating the small fishes that would prey on the larvae. In northern lakes, larval Bluegills move into the pelagic zone immediately after hatching to feed on zooplankton and remain there until about 12–14 mm SL (Werner & Hall 1988). The initial move into the pelagic zone is likely an effect of Largemouth Bass predation, in that the presence of bass forces juvenile fishes (which would prey on larval fishes) out of the pelagic and into the littoral zone, creating a predator-free space in the pelagic zone for larvae or early juveniles. Movement back into the littoral zone is likely due to the increased predation risk caused by increased pigmentation and a larger body size. Similarly, in pools of Brier Creek, Oklahoma, survival of larval centrarchids and cyprinids was low in pools that contained juvenile centrarchids and cyprinids, but significantly higher in pools with adult Largemouth Bass (Harvey 1991a). Larvae were generally in deep pools, or deeper sections of pools, where the presence of a predator had reduced or eliminated juvenile fishes. Juvenile fishes were shifted to shallow water habitats where predation from Largemouth Bass would be limited both by access and by risk of predation on the bass by terrestrial predators (Fig. 1.16). Likewise, Smallmouth Bass impacted larval fish survival in a larger river, Baron Fork of the Illinois River, Oklahoma (Harvey 1991b). Even with relatively high rates of larval drift, natural pools with adult bass had higher larval densities than did pools lacking adult bass, again suggesting the importance of the predator-free zone for larval survival.

In addition to habitat shifts, activity periods, such as foraging time, also may be affected by the risk of predation. Longnose Dace in two Canadian streams foraged almost exclusively at night; this pattern was maintained throughout the ice-free season. Although not tested directly, the nocturnal foraging pattern, which is rare among cyprinids, was attributed primarily to increased risk from avian and fish predation during the day (Culp 1989). Shifts in habitat use as a consequence of the threat of predation also can alter the presence or strength of competitive interactions. For instance, the crowding of small fishes in the littoral zone due to the threat of bass predation may cause increased competitive interactions in streams (Gorman 1988b) and lakes (Werner et al. 1983a), an effect experimentally demonstrated in ponds (Mittelbach 1988).

Life history attributes, including body size and age at maturity, can be impacted by predation pressure and thus affect the size structure and population dynamics of local fish assemblages. The Utah Chub (*Gila atraria*) comprises two distinct clades resulting from an Early Pleistocene divergence between the upper Snake River and the Bonneville Basin. The Utah Chub in the Bonneville Basin evolved in the presence of their primary predator, Cutthroat Trout, but those populations became predator free when Utah Chub populations became fragmented during the Late Pleistocene recession of Lake Bonneville beginning about 10,000 years ago. In contrast, Utah Chub populations in the Snake River have co-existed continually with Cutthroat Trout, producing a predator phenotype. The predator phenotype of the Utah Chub has higher juvenile growth rates, reaches a larger adult size, and is longer lived than the derived predator-free phenotype. In addition, the predator phenotype matures later and at a larger body size and has lower female reproductive effort (suggesting a tradeoff between reproductive effort and lifespan) compared with the predator-free phenotype (Johnson & Belk 1999; Johnson 2002).

Facilitation and Mutualism

In our discussion of species interactions we primarily focused on symmetrical negative interactions like competition or asymmetrical (+/–) interactions like predation. In this section we show that positive interactions (+/+; +/0) among fish species are also common and of potential importance to the formation and maintenance of fish assemblages. Facilitative interactions are asymmetrical or symmetrical positive encounters among organisms that benefit one or more of the participants and do not harm either (Stachowicz 2001). For instance, the predator-free zone provided to larval fishes by large, predatory fishes is an example of facilitation involving habitat modification. Facilitative interactions also may be symmetrical (mutualistic) when both species benefit from the association (e.g., Boucher et al. 1982). The terminology of interspecific interactions is complex; for simplicity, we follow Boucher et al. (1982) in dividing mutualistic behavior into direct and indirect mutualisms. In the former, direct interaction occurs between two species. In the latter, no direct contact occurs, but each species benefits from the other's presence. Direct mutualisms can be further subdivided into symbiotic and non-symbiotic mutualisms with the distinction between them based on the level of their physiological integration. Boucher et al. (1982), although acknowledging exceptions are frequent, considered that symbiotic mutualisms tended to be co-evolved and obligate, but non-symbiotic mutualisms tend to be facultative and not co-evolved. Much of the earlier literature on species associations treated mutualism as an obligatory response. Nevertheless, various studies (Gomulkiewicz et al. 2003; Hay et al. 2004) indicate mutualisms are often context dependent and may be obligatory in one area but not another and may even change to antagonistic interactions.

Facilitation and mutualism in fish assemblages can occur between fishes and other taxa, especially with foundation species (species that contribute a framework for the entire community, such as trees, grasses, or beaver [*Castor* spp.]; Bruno et al. 2003; Pollock et al. 2003), or only among fishes. Although we focus primarily on the latter, others provided evidence of a diffuse mutualism between species of *Oncorhynchus* and the trees surrounding the natal streams (Hay et al. 2004; Drake et al. 2006; Gende et al. 2007). Streams that are forested support greater densities of juvenile salmon because of the input of nutrients from leaf litter and instream wood. Spawning runs of adult salmon import large quantities of marine-derived nutrients (nitrogen, carbon, and phosphorus) via their post-spawning carcasses and thus subsidize growth of riparian trees. Similarly, significant transport of marine nitrogen into grape vineyards occurs via spawning migrations of anadromous Chinook Salmon and movement of carcasses onto the terrestrial landscape by scavengers (Merz & Moyle 2006).

Species Associations and the Potential for Facilitation

If co-existing species always segregated into distinct use of resources (Werner et al. 1977; Ross 1986), they would overlap minimally in use of space or foods, and individuals would occur most often with conspecifics and not in mixed-species groups. Even so, mixed-species contact groups are common in North American fish assemblages with two or more species of fishes occurring in a small space or with individuals intermingled. Suggestions of mixed-species interactions among freshwater fishes are not new. Reighard (1920) described minnow and Northern Hogsucker (*Hypentelium nigricans*) feeding interactions in detail, and also commented that he had observed the White Sucker (*Catostomus commersonii*) to be much less easily startled when accompanied by a group of Logperch (*Percina caprodes*). Although perhaps lacking proof, Reighard in this one paper suggested both enhanced feeding and safety as benefits from mixed-species groupings. In 1 m^2 plots in a small Minnesota lake, 14 significant negative species associations existed compared with 3 significant positive associations (Moyle 1973). Six of the negative associations were between minnows and piscivorous centrarchids. Positive associations between the Mimic Shiner and Bluntnose Minnow (*Pimephales notatus*), the Bluntnose Minnow and White Sucker, and the Common Shiner (*Luxilus cornutus*) and White Sucker suggested that some fish species were attracted to others by the protection and feeding advantages that a large school of fishes offers and that mixed-species schooling was common in this lake. Multispecies schooling occurred among four minnow species in a small Wisconsin stream, and observations in aquaria suggested that *Notropis* spp. are mutually responsive with individuals of one species readily following those of another (Mendelson 1975). Young of the Longnose Dace and Creek Chub often formed mixed schools in streams (Copes 1983). In Florida canals, Largemouth Bass ≤30 cm TL and similarly sized Bluegills form mixed-species foraging groups (typical group size of five) that interact in hunting small poeciliids and cichlids (Annett 1998).

We have already discussed studies documenting vertical habitat segregation of fishes. Here, we emphasize that species in benthic or water-column guilds often show little if any intraguild separation in habitat use (e.g., Grossman & Freeman 1987), although this is certainly not always the case (e.g., Baker & Ross 1981). The frequent lack of intraguild resource differences at least suggests that species in a guild often occur in mixed-species schools as documented in Coweeta Creek for several minnow species and Rainbow Trout (Freeman & Grossman 1992) and for six pool-dwelling minnow species in an Ozark creek (Gorman 1987, 1988ab). For these mixed-species groups, Gorman suggested both facilitation of feeding and enhanced anti-predator effects and that microhabitat use within the guild was a dynamic balance between segregation (lessening interspecific competition for resources) and associations (with potential benefits to mixed-group members). Ozark stream minnows clearly may segregate partially into distinct microhabitats, but this segregation is modified by the presence of other minnow species with slightly more positive associations (i.e., converging to common habitats when mixed species were present) than dissociations (i.e., avoidance of each other in mixed-species pairings) (Gorman 1987, 1988ab). In another small Ozark stream, species often formed mixed schools, intermixed vertically and horizontally (McNeely 1987).

In virtually all aquatic habitats, capturing >1 fish species in a single seine haul is more common than not (raising the issue of whether the sampling method is capturing fishes across more than one microhabitat, or whether species are occurring in mixed associations), but direct visual observation by snorkeling also suggests the preponderance of mixed-species groups, especially for minnows. In a total of 787 seine hauls or snorkeling observations made in diverse habitats from large rivers, Lake Texoma, Oklahoma (a large reservoir), and smaller streams, 71% included >1 minnow species. Included in these samples were small seine hauls, about 10 m^2 each, in the Canadian River, Oklahoma (Matthews 1977), in which 71% had 2 species and 46% had ≥3 species present. In 20 m shoreline seine hauls in Lake Texoma (Matthews 1998), 86% had ≥2 minnow species, and 60% contained ≥3 minnow species. In 2 m^2 kickset seine hauls (Roanoke River, Virginia, Matthews et al. 1982a), 55% had ≥2 minnow species present (WJM unpubl. data). The trend for mixed-species groups of minnows also was found in additional small streams of south Oklahoma and in the Arkansas Ozarks

(Matthews 1998). Such examples of mixed-species occurrences in localized field samples do not yield information on actual interactions among species but do suggest the possibility that North American minnows could form mixed-species groups under a wide range of conditions. Thus, in North American lakes or streams it is common to find ≥2 related fish species in such close proximity to each other that information transfer or interactive benefits seem possible.

Facilitation and Mutualism in Fish Assemblages

Proposed benefits from interspecific aggregation include increased foraging efficiency and enhanced detection and avoidance of predators (Boucher et al. 1982). Early-warning benefits in mixed groups are well known in some organisms such as birds (Thompson & Thompson 1985). Fish in monospecific shoals (i.e., schools) transfer information about predators (Magurran & Higham 1988), but early warning would be effective in a mixed-species shoal only if information is transmitted rapidly (Godin et al. 1988). In mixed-species shoals, competition for food might be less intense than in a monospecific shoal while presenting a predator the impression of a large shoal. A possible cost of mixed-species shoaling is incurred if predator evasion maneuvers were impeded by heterospecifics (during an actual predator attack) (Pitcher 1986). Also in mixed-species shoals one species might facilitate access to prey by another, or feeding opportunities might be improved by observation of feeding by heterospecifics (Pitcher 1986). For example, in North American streams, if one species of Sunfish (genus *Lepomis*) strikes at an insect on the surface of a pool, other Sunfish species rapidly approach to feed. In multispecies assemblages, temporarily rare species might persist by virtue of hiding within schools of more abundant heterospecifics (Moyle & Li 1979). By joining mixed-species groups, a fish might enjoy the benefit of being a member of a larger group (anti-predation; vigilance) yet reduce the cost of intraspecific competition to less than it would be in an equally large group of conspecifics (Allan 1986). In an artificial stream, Allan (1986) tested three sympatric European cyprinids that often formed mixed-species shoals in streams (Dace, *Leuciscus leuciscus*; European Minnow, *Phoxinus phoxinus*; and Gudgeon, *Gobio gobio*) and suggested that altered behaviors of the species in mixed aggregations reflected a balance between the tendency to avoid identical use of resources, yet to remain close enough to the other species to gain anti-predation benefits from the appearance of a large shoal.

Some species in mixed groups may benefit from feeding actions of others. When benthic feeding fishes like Suckers (Catostomidae) disturb substrata, they may increase the accessibility of invertebrates to smaller insectivorous fish species. Bigeye Shiners swim above schools of benthic-foraging Ozark Minnows, feeding on items that were suspended in the water column, and Hornyhead Chubs follow the benthic algivore, Central Stoneroller (Gorman 1988b). Similarly, Gilt Darters (*Percina evides*) commonly follow two other darters, Logperch and Blotchside Logperch (*P. burtoni*), feeding on items exposed when the logperches flip over stones (Greenberg 1991). In clear upland streams, minnows (e.g., Blacktail Shiners) commonly closely follow large Northern Hog Suckers, as suggested by Reighard (1920), feeding on invertebrates suspended by benthic feeding of the Sucker (Baker & Foster 1994). In this relationship, the larger, benthic-feeding species might also benefit if it received early warning of a threat if the smaller fishes took flight from a potential predator. If this is beneficial to both participants, then the Hog Sucker–minnow tandem might represent a true mutualism.

In addition to potential benefits from interactions of species in feeding or general predator defense, examples of more complex interspecific groupings exist, providing positive benefits to one or both members of the association. For instance, nest associations (Wallin 1989, 1992; Johnston & Page 1992; Johnston 1994ab) are observed frequently in North American streams. In many, visiting species lay eggs in or on gravel nests or other structures that are tended by the original (often larger) builder. For example, numerous chub species (genera *Nocomis*, *Semotilus*) build large gravel nests on which other minnow species spawn. The minnow eggs apparently benefit by being in clean gravel of the nest or from protection by the guarding nest owner. Hornyhead Chub nests are piles of gravel up to 0.9 m across and 0.3 m tall, constructed by the host carrying stones some distance by mouth and forming quite prominent structures in the gravel substrata of small streams (Robison & Buchanan 1988). Nests of *Semotilus* also are used frequently as spawning sites by other species. Creek Chubs construct pit-ridge nests (Reighard 1910; Ross 1977a; Maurakis et al. 1990; Johnston & Page 1992) where the male initially excavates a spawning pit about 7 cm deep by shoving stones away or moving them with his mouth. Males are multiple spawners and on each successive spawning the male extends the pit farther downstream, covering the newly laid eggs with stones from the extended pit. As this process continues, the result is a longitudinal ridge of pebbles (about 69 cm long × 22 cm wide × 4 cm high) that covers the fertilized eggs with the active spawning pit at the downstream end.

Nest associates can gain improved reproductive success by spawning over host nests. The associates do not necessarily respond to the nest substratum but to the presence and activity of the host (Johnston 1994a). In an experiment that consisted of constructing artificial gravel-mound nests in two streams (to mimic nests of the Bluehead Chub, *Nocomis leptocephalus*, and Green Sunfish, which naturally spawned in the streams), the artificial nests were unused by any of the numerous minnow species (including Central Stoneroller; Rosyside Dace; and Greenhead Shiner, *Notropis chlorocephalus*) that were observed spawning over natural nests in the streams (Johnston 1994a). In contrast, Topeka Shiners, a nest associate with Sunfish (genus *Lepomis*), apparently also spawn in the absence of Sunfish nests, as shown by males selecting and defending spawning sites over sand substrata (Witte et al. 2009). The association between the Yellowfin Shiner (*Notropis lutipinnis*) and Bluehead Chub may be a true mutualism because Yellowfin Shiners failed to reproduce in the absence of chubs. Bluehead Chub eggs also may benefit because repeated, vigorous activity by spawning minnows may keep sediments from accumulating in the nest, but advantages gained by the host were not directly tested (Wallin 1989, 1992). The hypothesis that the host also gains improved reproductive success in the presence of a nest associate was supported with the nest associate, the Redfin Shiner (*Lythrurus umbratilis*), the Green Sunfish host, and a predator (on eggs and larvae), the Longear Sunfish (*Lepomis megalotis*) (Johnston 1994b). In the presence of the predator, Green Sunfish nests that had associates present showed higher larval Sunfish survival than in those without associates, clearly indicating that hosts accrue benefits from the nest associate and that the association is a true mutualism. In tests without the predator present, no difference existed in survival of Green Sunfish larvae in nests with and without associates, indicating that associates were not detrimental to the host. The benefit of the associates to the host in the presence of a predator was likely achieved through a dilution effect.

Whether or not suggested mutualisms are fortuitous interactions or arise from co-evolution is difficult to discern, in part because views differ substantially on what constitutes co-evolution. Ehrlich & Raven (1964) used the term in the sense of tightly coupled species pairs with evolution of a given trait in one species producing subsequent evolution of a trait in the other species of the pair, which results in selective pressure producing further modification of the trait in the first species, and so on. An alternate view to tightly coupled co-evolution of pairs is that diffuse co-evolution could affect entire assemblages of species simultaneously. That is, communities could evolve by virtue of overall contacts among species without involving reciprocal evolutionary steps by all species (Inouye 2001). Other views of co-evolution include geographic mosaic models based on different co-evolutionary outcomes for populations in different communities (e.g., Thompson 1994, 1999ab, 2005; Gomulkiewicz et al. 2000; Nuismer et al. 2003). Tightly and loosely coupled co-evolution are quite different phenomena, and co-evolution of communities is controversial (Krebs 1994), resulting in a huge primary literature and numerous major summaries (e.g., Gilbert & Raven 1980; Thompson 1982, 1994, 2005; Futuyma & Slatkin 1983; Stone & Hawksworth 1986). In fish assemblages, the term "co-evolution" most often implies diffuse co-evolution or merely that members have traits influenced by long-term general associations with others (e.g., MacLean & Magnuson 1977; Gorman 1987, 1988a; Wikramanayake & Moyle 1989; Matthews 1998), although Baltz & Moyle (1983) suggested that habitat segregation between two species (Rainbow Trout and Sacramento Sucker) was due to their long history of co-evolution.

In the section on the origin and age of fish assemblages, we demonstrated that species comprising local assemblages are often of widely different evolutionary ages and that fish assemblages have gained and lost species over evolutionary time scales. Because of this, the likelihood of a suite of species remaining together over long periods of time (i.e., 1,000s of years) is seemingly low. Similar arguments are given by others (Matthews 1998, Chapter 9; Grossman & Freeman 1987; Grossman et al. 1987ab, 1998) who suggested from multiyear studies that habitat availability, environmental disturbance, predation, or independently evolved species traits dominate microhabitat use by individual species in streams. Grossman & Ratajczak (1998) argued that stream fish communities are not highly co-evolved systems so that interactions among species are not regulated by strong or consistent interspecific interactions.

For co-evolution to be important, species should have a high encounter rate (Thompson 1982; Price 1984), interspecific interactions should not be weak or of short duration (Futuyma & Slatkin 1983; Farrell & Mitter 1993), and substantial periods of close association should prevail (Brown 1995). Interactions, hence selective pressures of one species on another, change in the context of the other species present in a community, affecting mechanics of diffuse co-evolution (Inouye 2001). Habitat availability clearly is an important factor in species co-occurrence, or the degree of persistence of local assemblages. Certain habitats, like deep pools, can be critical to the stability of a fish community (Schlosser 1987; Fausch & Bramblett 1991; Lohr & Fausch 1997). In practice, whether fish species congregate consistently in a particular kind of habitat in response to past co-evolution of traits or more because of independently acquired traits, the likelihood of future trait modification by co-evolutionary interactions is increased if they now co-occur in regular, direct contact.

If a species at one location is part of a persistent suite of other species at the scale of years or decades, the probability increases that those species will consistently influence its evolution. Conversely, a species surrounded by a frequently changing milieu of other species is less likely to evolve under the influence of predictable biotic selection pressures (Futuyma & Slatkin 1983). What is lacking in many of the debates about co-evolution is empirical information on just how long (months, years, or generations) patterns of direct contact among mobile species in real-world communities must persist to provide a consistent template within which interspecific genetic adjustments of traits, hence local co-evolution, can occur. Some co-evolved relationships among organisms are assumed to be quite old (McNaughton 1984) or develop over long periods of intimate contact (e.g., 50 million years, Currie et al. 2003). Nevertheless, reviews (Thompson 1998, 1999ab, 2005) and empirical evidence (Thompson & Cunningham 2002; Palkovacs et al. 2009) show that co-evolutionary processes among species can operate at time scales of decades, not requiring long periods of geologic time (i.e., rapid co-evolution). Thus, observations of persistent contacts in ecological time (e.g., Matthews & Marsh-Matthews 2006b) can be pertinent to evolutionary processes for species and communities, and the duration of contact shown for pairs and triads of species in the section on persistence of assemblages could be sufficient for rapid co-evolution to occur.

The biology of individual species also influences the possibility of the acquisition of co-evolved traits. Having the potential for rapid genetic modification combined with short generation times increases the probability that fish co-existing in local communities at scales of years to decades could co-evolve. Genetic adaptation to changed temperatures apparently occurred in <50 years for the Red Shiner (Zimmerman & Richmond 1981), and mosquitofishes (*Gambusia* spp.) can have rapid local genetic change (Stearns 1983; Zimmerman 1987). Some fish species produce multiple generations/year. Red Shiners can reproduce in their first summer of life (Marsh-Matthews et al. 2002) resulting in two generations/year, and Western Mosquitofish can produce several generations/year. Many other small-bodied fishes (minnows, Topminnows, some Sunfishes) reproduce when they are a year old (Ross 2001). Consistent associations of such species with others for even a few years would have the potential to allow incorporation of genetic change through multiple generations if selection pressures were consistent.

SUMMARY

Pulling a seine through a riffle or pool of a stream, or snorkeling along a lake margin, reveals suites of fish species that are often unique in terms of kinds, numbers, and sizes of individuals. The basic composition of these local assemblages may vary along both spatial and temporal axes. The seemingly simple question of “Why do we see what we see?” turns out to be complex and best approached hierarchically (Fig. 1.2), beginning with biogeographic phenomena operating over large spatio-temporal scales and progressing through ecological phenomena at increasingly more localized spatio-temporal scales. The outcome of processes operating at evolutionary and ecological time scales results in what we see in a particular local assemblage at a given point in time and also explains the uniqueness of different assemblages and why it is important to conserve these temporally dynamic end-points of assemblage evolution and ecology.

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Chapter 2 Mating Behavior of North American Freshwater Fishes

Deborah A. McLennan

Behavior mediates four major components of evolution: what you eat (including how not to be eaten), where you live, with whom you mate, and what you do with the offspring resulting from those matings. In this chapter, I focus my attention on one of these components, sex. Breder & Rosen (1966) needed 675 pages to describe the known reproductive behaviors of fishes at that time. Our knowledge has increased many times over in the past 48 years, so it is clearly beyond the scope of this chapter to discuss everything we now know, or think we know, about the breeding behavior of North American freshwater fishes. This chapter is therefore somewhat eclectic, a reflection of the things that fascinate me the most about the sexual behavior of fishes. I discuss sensory systems, what to do with eggs, and alternative mating strategies. Along the way I present several large tables, which the discerning reader will note I do not discuss in detail. These tables are provided to demonstrate the extent of our knowledge with the hope that young researchers will be stimulated to boldly go where no ichthyologist has gone before in their quest to understand fish behavior.

FINDING EACH OTHER: COMMUNICATION GOES MULTIMODAL

Fishes are immersed in a whirlwind of sensory stimuli. Every species, however, responds to only a fraction of that whirlwind, allowing conspecifics to recognize and locate one another in what might otherwise be a chaotic universe. The intuition that the sensory whirlwind was partitioned in a species-specific manner was a critical prerequisite to formulating concepts of reproductive isolation, mate recognition, and sexual selection. More recently, biologists have begun to recognize that communication is often a multifaceted dialogue, a complex interchange of signals within (multicomponent, Holldobler 1995; Johnstone 1995, 1996) and among (multimodal, Guilford & Dawkins 1991ab; Rowe & Guilford 1999) sensory modalities. Such complexity serves many functions. Multiple signals may convey the same information, thus increasing the probability of both transmission and reception by decreasing the amount of degradation in the channel and by repeating the same message in many different ways (increasing redundancy, Shannon & Weaver 1949). Multiple signals also may convey different bits of information pertaining to a larger message (multiple messages, Johnstone 1996; Rowe 1999 and references therein). If complexity functions to increase the reliability of message transmission and perception, then presumably one way to increase that complexity is to send redundant and complementary information in as many sensory modalities as possible (Tavolga 1976). Here, I discuss what we know about the roles of vision, olfaction, and sound in the reproductive biology of freshwater fishes.

VISION IN COURTSHIP

When some people think about North American freshwater fishes, they immediately conjure up images of landing a record-setting bass or trout. Others see spectacularly colored darters, Sticklebacks, and minnows (at least I do). In other words, we tend to think visually. Unsurprisingly, given our perceptual biases, most of the research about the evolution of mate recognition and discrimination in freshwater fishes has concerned visual cues, in particular the importance of body size and nuptial coloration.

Body Size

From male and female perspectives, the general rule of thumb appears to be bigger is more preferred (e.g., Rock Bass, *Ambloplites rupestris*, Sabat 1994b; Smallmouth Bass, *Micropterus dolomieu*, Hanson & Cooke 2009; Threespine Stickleback, *Gasterosteus aculeatus*, Rowland 1982, 1989b). Preference for a larger-bodied mate makes sound evolutionary sense for both sexes. Female fecundity in fishes is often correlated strongly with size, and larger males tend to make better fathers because they more effectively defend the nest from intruders and/or ventilate eggs in longer and more frequent bouts (e.g., Wiegmann & Baylis 1995). In fishes in which males invest nothing but sperm in the next generation, body size may indicate genetic quality. For example, large males of the Panuco Swordtail, *Xiphophorus nigrensis*, are better swimmers than small males and should be able to more effectively evade predators (Ryan 1988).

One of the best-studied examples of mate choice based on body size comes from a clade of swordtails and platys (Poeciliidae, Liverbearers: genus *Xiphophorus*) distributed throughout Mexico. In many species of *Xiphophorus* males develop an extension of the lower caudal fin rays to form an elongated, sword-like structure that often is decorated with yellow, green, or orange stripes flanked by black (Fig. 2.1; Basolo 1995a), enhancing its conspicuousness. Swords evolved in the context of a pre-existing bias in the female's visual system (sensory bias or exploitation, Ryan 1990ab, 1997, 1998); females from both sworded (Green Swordtail, *Xiphophorus helleri*; Fig. 2.1) and swordless (Southern Platyfish, *Xiphophorus maculatus*; Variable Platyfish, *Xiphophorus variatus*) species, as well as from the swordless sister-group to *Xiphophorus* (Olmec Priapella, *Priapella olmecae*) prefer males with swords (Basolo 1990, 1995ab; Trainor & Basolo 2000). The preference, in turn, is apparently the outcome of a more general response to large body size (males with swords look bigger) because the preference can be overridden by increasing the size of a swordless male relative to his sworded rival (Haines & Gould 1994; Rosenthal & Evans 1998). A similar dynamic is known for another poeciliid, the Sailfin Molly, *Poecilia latipinna*. Male Sailfin Mollies have large dorsal fins (hence the name), which they flare during courtship (Fig. 2.2). Females prefer large-bodied males (dorsal-fin size constant) (Schlupp et al. 1994; Ptacek & Travis 1997; Gabor 1999); however, that response is nullified when a small male with a big dorsal fin is offered as an alternative. Females also prefer males with bigger dorsal fins (body size held constant), but that preference vanishes in the presence of a larger, finless male. The surface area of the male's total lateral image (body and dorsal fin) is evidently the critical factor in mate choice based on size; how that area is apportioned into body depth and fin height is relatively unimportant at least for these two variables

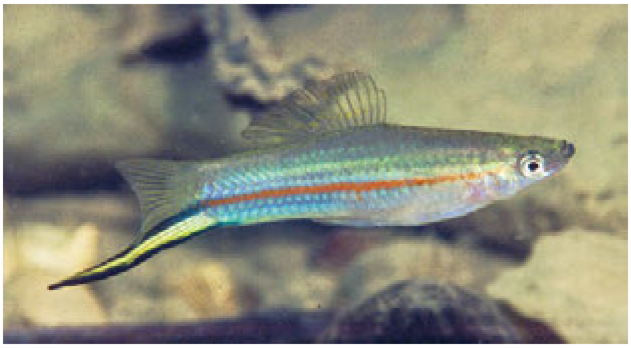

Figure 2.1. In the Green Swordtail, *Xiphophorus helleri*, as well as in other species in the genus, males have an extension of the ventral caudal rays, producing an elongate, sword-like structure that is variously brightly colored (see also Fig. 2.6). The sword increases the female's visual perception of the male's size, and hence, males with long swords are preferred by females over males with short swords when body size is held constant (male, Rio Tulija, Rio Grijalva-Usumacinta drainage, Chiapas, Mexico, 1998; photograph by and used with permission of Juan M. Artigas Azas).

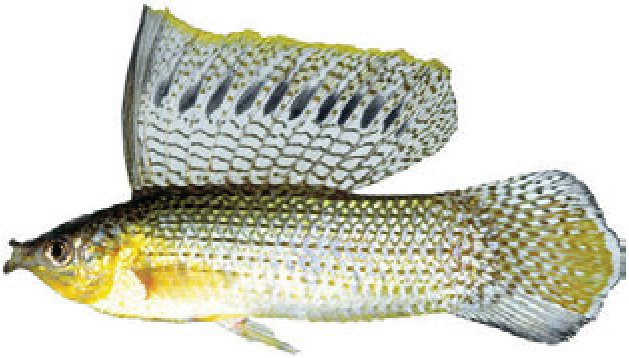

Figure 2.2. Male Sailfin Mollies, *Poecilia latipinna* (about 70 TL), have extremely enlarged dorsal fins that are flared during courtship. Females have much smaller dorsal fins. Female preference for breeding males is complexly affected by interactions of fin size and body size (male, ditch between Otter Creek and Cedar Key, Route 24, Levy County, Florida, 16 June 1995; photograph by and used with permission of Noel M. Burkhead).

(MacLaren et al. 2004; MacLaren 2006; same result using Shortfin Molly, *Poecilia mexicana*, females, MacLaren & Rowland 2006). This is a familiar theme in intersexual selection; females are attracted to bigger males (Staddon 1975; Ryan & Keddy-Hector 1992), possibly for the simple reason that size and percent retinal stimulation are correlated (O'Brien et al. 1976, 1985; Rowland 1989ab; MacLaren 2006), which establishes the pre-existing bias in the female's sensory system (for a fascinating complication, see the Sheepshead Swordtail, *Xiphophorus birchmanni*, in which females prefer males with large bodies but short dorsal fins and swords, Fisher et al. 2009 and references therein).

The sensory bias is tapped further by male courtship behavior in swordtails. Female Green Swordtails prefer videotapes showing courting males, rather than males engaged in any other activities (Rosenthal et al. 1996a). Male courtship involves a series of stereotyped displays, including a backward swim in which the male lashes his caudal fin and sword from side to side in front of the female. This display is detected by pathways in the teleostean optic tectum that are sensitive to directional biases in moving images (Guthrie 1990). Thus, the static (size, possibly contrast and conspicuousness of the sword) and dynamic (movement) components of the male as a courtship unit trigger a response from the female by taking advantage of the way her visual system is designed from sensory cells in the retina to neural processing and interpretation of that sensory input in the midbrain (Rosenthal et al. 1996a).

The evolution of large body size and the sword is influenced by more than just sexual selection. The predatory Mexican Tetra, *Astyanax mexicanus*, also shows a visual bias toward sworded males (Rosenthal et al. 2001, 2002a). Sensory bias toward something as basic as large size (retinal stimulation) is likely to be a taxonomically widespread phenomenon, so a natural selection vector from increased predation pressure will oppose any sexual selection vector favoring increased size. The strength of this opposition will be weakened if larger individuals have a higher probability of escaping predators despite being detected more readily by them (e.g., stronger swimming of large Panuco Swordtail males, Ryan 1988).

Overall then, the evolution of body size (with the sword) in swordtails reflects the outcome of a dynamic interaction between benefits and costs. The benefits are threefold: large males are better competitors, they are stronger swimmers, and females prefer them. The costs include being more visible to predators and the increased metabolic costs from longer swords on swimming and courting (Basolo & Alcaraz 2003; Kruesi & Alcaraz 2007; Cummings & Gelineau-Kattner 2009). Because of this dynamic interaction, sword presence or absence and absolute length will be sensitive to environmental and social factors and should vary both across and within species of the swordtail clade.

Exceptions to Body-Size Preference

Given a general preference for large size in many freshwater fishes, are there cases in which that preference can be overridden? The answer is yes, under unusual and possibly clade-specific circumstances. For example, male Mottled Sculpins (*Cottus bairdii*) are larger than females and provide all of the parental care (this is typical in *Cottus*, Smith 1923). Males compete for access to breeding territories, and then sit under their rocks, awaiting the approach of a gravid female. A female may visit several males before choosing her mate and depositing her clutch (about 33% of body weight, Hann 1927) on the ceiling of his rock (Bailey 1952; Downhower & Brown 1977, 1979; Brown & Downhower 1982). Males invest ≤30% of their fat and protein reserves defending their offspring from egg predators, especially female conspecifics (Morris 1955; Savage 1963; Downhower & Yost 1977). This high level of investment is repaid in confidence of paternity; DNA microsatellite markers indicated that guarding males sired 98% of the fry in their nest (23 nests, 1,259 offspring, Fiumera et al. 2002). A female spawns only once during the breeding season (Hann 1927; Savage 1963), so her choice of a partner is a critical determinant of her fitness. That choice is based on male body size; egg survivorship increases with paternal size, so the bigger the male the better the father (Downhower & Brown 1980; Brown 1981). This benefit, however, must be balanced against the costs of searching for a male (time, energy, increased predation risk) and the cost associated with being the last female to spawn with him (survivorship of the last clutch is about half that of the clutch immediately before it) (Downhower & Brown 1981; Brown & Downhower 1983). Part of that balancing act includes the incorporation of information about the last male the female has visited in a relative rule: if he is larger than the last male, spawn; if he is smaller, keep moving (Brown 1981; Downhower & Lank 1994). The preference, however, has a twist because male Mottled Sculpins will eat small females. Unsurprisingly, small females try to avoid being eaten by courting less-preferred small males, so the distribution of male mating success cannot be predicted from male body size alone

(Downhower et al. 1983). Another member of the genus, Kankyo-kajika, *Cottus hangiongensis*, is not cannibalistic and, predictably, the correlation between male size and reproductive success is stronger (Goto 1987).

Female preference for large body size also may be overridden by mate-choice copying (Dugatkin 1992, 1996, 1998). Copying is studied by placing a female where she can see, but not smell or interact with, two males. After the female's preference is determined (measured by the male she spends the most time near), a model female is placed next to the non-preferred male and the test female is allowed to watch the two for a period of time before being allowed to choose again. In theory, copying may be adaptive if there is a high cost to assessing mates, if females differ in their assessment abilities (e.g., young females are worse assessors than older, more experienced females), or both (Waltz 1982; Dugatkin & Godin 1993).

Within North American freshwater fishes, most mate-copying research has focused on the Sailfin Molly (Fig. 2.2). Copying over short time periods with just one model female occurs when the males are both matched for size. In this case, the test female presumably has a more difficult time making a decision since she is getting no useful information from body size, so she opts for copying another female who presumably saw something she missed. Interestingly, the female remembers the male for ≥24 h after seeing him consorting with another female, which implies that these fish have greater memory storage and retrieval abilities than previously thought. Ability to remember is important because a female's opportunity to mate with the preferred male in the field may often be interrupted by predators, conspecifics, and foraging activities (Witte & Ryan 1998; Witte & Massman 2003). Copying behavior also extends from the acceptance into the rejection arena. Females who have watched a male's courtship advances be spurned by another female spend less time with that male when allowed to choose (Witte & Ueding 2003).

What happens if the males are not matched for size? Female Sailfin Mollies from two different populations show a strong preference for large over small males, which is stable across time (Travis 1994; Marler & Ryan 1997; Witte & Ryan 1998, 2002; Witte & Noltemeier 2002). Can that preference be switched to the smaller male by a copying dynamic? In Sailfin Mollies, the answer seems to be no if females see only one female near the small male, but yes if they see >1 female visit the small male sequentially, or if they see just one female near him for an extended period of time. Hence, female Sailfin Mollies use a series of decision-making rules that place a genetic predisposition for a particular male trait (large size) within a larger social context. This is a critical discovery because it means that the effects of nature (genes) can be modified by nurture (in this case, learning) so that a strict preference need not reach its fullest potential in a naturally breeding population.

The effect of context-dependent copying may serve ultimately to reduce the consistency of female choice and weaken the influence of sexual selection (e.g., experiments with the Guppy, *Poecilia reticulata*, Dugatkin & Godin 1992; Perugia's Limia, *Limia perugiae*, Applebaum & Cruz 2000). This begs the question of how often females in a natural population are exposed to mate-copying situations that would counter their normal biases. These data are needed because the two dynamics, copying under conditions of limited information (males closely matched) or copying leading to reversals of female preferences, have different evolutionary implications.

Nuptial Coloration and Limits of Vision

Light transmission is much more complicated in aquatic ecosystems than in air (e.g., Levine et al. 1980; Lythgoe 1980). Depending on their wavelength, photons are absorbed or scattered by water molecules, organic particles, phytoplankton, and other plants. Absorption of light on its way from the object to the eye leads to image degradation because information is missing. The scattering of photons from other sources into the visual pathway decreases contrast between the object and the background so that distant objects appear faint and blurred, as if covered by a veil or fog (the veiling effect). Scattering of light thus leads to image degradation because some information is lost (from the object) while irrelevant information is added (from the background). So, the composition of light in any given environment is dependent on the distance that light has traveled since entering the water and what is in the water. For example, chlorophylls and other organic substances absorb most light at depths of about 25 m and shift the transmission maximum to wavelengths (λ) of about 500–600 nm (greenish-yellow: majority of coastal waters, lowland ponds, rivers). Add tannins and lignins to the picture, and little light penetrates >3 m with the transmission maximum pushed to ≥600 nm (reddish-brown: swamps, marshes, tropical blackwater rivers). Because of the differential transmission in these systems, the quality (intensity and λ composition) of light may vary dramatically along different lines of sight radiating from the same point (i.e., downwelling, upwelling, and horizontally scattered photons).

What do fishes see? In brief, most freshwater fishes have at least two types of light-sensitive pigments in their retinas. The peak spectral sensitivity of matching pigments matches the dominant background wavelength (spacelight). Objects reflecting the same wavelengths as the spacelight appear invisible, but objects reflecting other wavelengths will appear dark against the background. Light detected by offset pigments does not match the spacelight (hence the term "offset"), so objects reflecting these wavelengths appear bright against a darker background. The distribution of light-sensitive pigments in freshwater systems tends to track the light environment (e.g., shallow, clear waters—ultraviolet, blue, green, and orange-red pigments in diurnal poeciliids and cyprinodonts; greenish freshwaters—blue, green, and orange-red in diurnal Cichlids, minnows, Catfishes, and salmonids: Loew & Lythgoe 1978; Crescitelli et al. 1985). In the following I focus on the role of color in the male-female courtship dialogue. Given the variety of color patterns and our focus on visual signals, the most astonishing thing about research in this area is not so much what we have discovered (although that is, of course, fascinating), but rather that we have discovered so little.

How to Be Seen: Color in Killifishes

The Bluefin Killifish, *Lucania goodei*, inhabits a wide variety of freshwater habitats throughout (primarily) Florida (Fig. 2.3). These habitats range from clear waters in which all wavelengths are transmitted quite well, but short wavelengths (UV-violet) are transmitted most effectively, to turbid, tea-stained waters, an environment that favors longer wavelengths (yellow-red). Retinal design parallels these transmission differences. Bluefin Killifishes from clear springs have more UV and violet cones and higher concentrations of short wavelength-absorbing opsins (SWS1, SWS2B), and consequently fewer yellow and red cones and lower concentrations of long wavelength-absorbing opsins (Rh2, LWS), than do swamp dwellers (Fuller et al. 2003, 2004). Much of this variability is due to environmental effects, particularly the lighting conditions under which offspring are raised (Fuller & Travis 2004; Fuller et al. 2005).

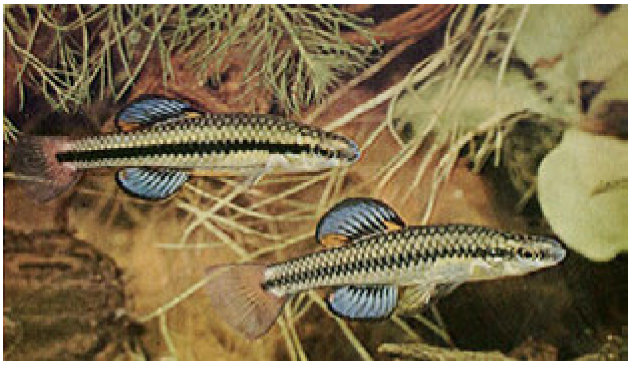

Figure 2.3. Male Bluefin Killifish, *Lucania goodei*, flare their colorful dorsal and anal fins to compete with other males for spawning sites and to court approaching females. The color of the fins and composition of photoreceptor pigments varies with water clarity; these fish occur in habitats as diverse as the clear waters of springs to the turbid, tea-stained waters of wetlands (picture courtesy the Calypso Photographic Library, www.calypso.org.uk).

Male Bluefin Killifish (Fig. 2.3) compete for and guard patches of vegetation that serve as oviposition substrates. Fighting involves flaring the dorsal and anal fins before proceeding to a circle fight. Once established, a male courts an approaching female by flaring his fins and swimming in circular loops around and in front of her. Females visit several males before spawning and spawn many times over the breeding season (Fuller 2001). Males develop a red dot at the base of their caudal fins and blue pigmentation in the anterior three-quarters of their dorsal fins. The remaining part of the male's dorsal fin may be blue, red, or yellow; the pelvic fins are either red or yellow; and the anal fins may be red, yellow, blue, red and blue, or yellow and blue. Some color combinations (yellow-blue and to a lesser extent red-blue anal fins) in this extreme polymorphism were predicted by drainage or longitude. Males with red, and to a lesser extent, yellow anal fins were more common in clear springs. Because spring fish are more sensitive to short wavelengths, the red-yellow signal appears dark against the bright blue spacelight (contrast). Males with blue anal fins were more common in swamps (Fig. 2.3). In swamps, the male's anal (and dorsal) fin color would appear quite dull because short wavelengths are attenuated quickly, and the fish themselves have a retina set to detect yellow-red. Even if this maximizes contrast (blue fins, dark, against red spacelight, bright), the signal will not be transmitted far nor will it be detectable by a potential mate from a distance. This paradoxical result might indicate a need for up close and personal communication; i.e., perhaps the cost of attracting predators from a distance is greater than the benefit of attracting females (Fuller 2002).

So, what factors are maintaining such a variety of male color morphs? Investigations using red and yellow males indicated that females do not choose mates based on color (McGhee et al. 2007), level of male aggression and fertilization success are not correlated with color (Fuller 2001; Fuller & Travis 2001), and negative frequency-dependent mating success (rare male effect) is not operating in the field (Fuller & Johnson 2009). Given the environmentally based plasticity in visual pigments, the fitness of a given color morph possibly varies across different spectral environments, such that each morph will have the most reproductive success where it is most conspicuous (Chuno et al. 2007; Gray et al. 2008). Tests of this hypothesis, which will require more complicated control of lighting conditions in the lab, should prove fascinating.

Problems with Patterns: Color in Darters

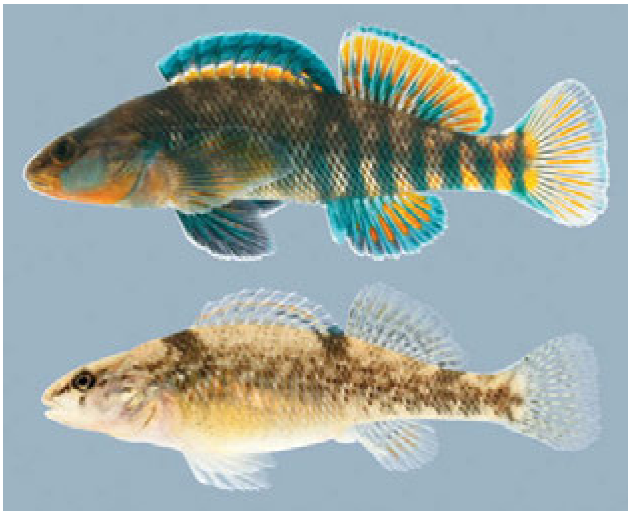

Figure 2.4. Like many species of darters (family Percidae), breeding male (*top*) Rainbow Darters, *Etheostoma caeruleum*, develop bright nuptial coloration during the spring, while females (*bottom*) remain comparatively cryptic. Nevertheless, even though sexual dichromatism is widespread among darter species, the actual function of male color (e.g., male-male interactions, female courtship) is not well understood (male and female, Vermilion River, Vermilion County, Illinois, May 2009; photograph by and used with permission of Uland Thomas).

Darters (Percidae, Perches) are among the most complex and flamboyantly colored of North American freshwater fishes (Fig. 2.4). Surprisingly, no correlation is known between the intensity of carotenoid-based colors (yellows, oranges, and reds) and male reproductive success (Orangethroat Darter, *Etheostoma spectabile*, Moerchen 1973; Pyron 1995; Striped Darter, *Etheostoma virgatum*, Porter et al. 2002; but see Reeves 1907 and Page 1974). This does not rule out a role for color in male-male interactions or the possibility that other components of the male signal, perhaps blue- or green-based colors or contrast independent of color, are used by females to assess male suitability. For example, females from two Rainbow Darter (*Etheostoma caeruleum*) populations (Prairieville Creek and Seven Mile Creek, Michigan) performed more nosedigs, a measure of female sexual motivation, near Prairieville Creek males. Prairieville Creek males were smaller but appeared to display a greater red-blue contrast than did the larger, darker Seven Mile Creek males (Fuller 2003). Females from several darter species preferred larger males (Spottail Darter, *Etheostoma squamiceps*, Bandoli 1997; Relict Darter, *Etheostoma chienense*, Piller & Burr 1999; Fantail Darter, *Etheostoma flabellare*, Moretz & Rogers 2004), so the Rainbow Darter females' response was unusual, and perhaps, color related. To test this suggestion we would have to determine whether Rainbow Darter females do indeed prefer smaller males independently of color. If color patterns are not transmitting information about male condition that females can use to differentiate among conspecific suitors, perhaps the nuptial signal is acting in species recognition, a form of sexual selection involving discrimination between a conspecific and another species (Ryan & Rand 1993). Given, however, that about 25% of all darter species are introgressed, indicating hybridization occurred at some point in their evolutionary history, and that the dominant crosses within one genus, *Nothonotus*, are between egg-burying species in which the males are noticeably different in coloration (Keck & Near 2009), it is difficult to explain what role nuptial color plays in these enigmatic fishes.

Truth in Advertising: Color in Pupfishes

Territorial male Pecos Pupfish (*Cyprinodon pecosensis*) develop a metallic blue color over their entire bodies, but females and juveniles remain cryptically colored olive-brown, black-barred fish. A range of nuptial color develops from light blue with conspicuous lateral bars to intense blue and no bars. Male color development is context dependent; males do not develop the signal in isolation or in the presence of juveniles. The signal appears at low levels during agonistic interactions with other males then intensifies dramatically in the presence of a courting female and increases again after a spawning bout, reliably signaling, "I am a successful male; a female has already chosen me" (Kodric-Brown 1996; see also Threespine Stickleback, Reisman 1968; McLennan & McPhail 1990).

The intensity of blue also appears to be signaling more than just past spawning success. Relative to their dull-colored non-territorial counterparts (Kodric-Brown &

Nicoletto 1993), territorial males are much better swimmers, a measure positively correlated with metabolic efficiency and stamina (Smit 1965; Beamish 1978; Stahlberg & Peckmann 1978), and are in better condition (i.e., heavier / unit length, Bolger & Connolly 1989). Within territorial holders, more intensely blue males are more aggressive and thus better at defending their territories from intruders (Kodric-Brown 1983; other examples of the intensity of color being correlated with dominance include the Crescent Gambusia, *Gambusia hurtadoi*, McAlister 1958, and Everglades Pygmy Sunfish, *Elassoma evergladei*, Miller 1963). Protection of the eggs is a byproduct of territory defense because males do not care for eggs and even indulge in limited egg cannibalism (Echelle 1973; Itzkowitz 1974; Loiselle 1982). Even as a byproduct, such protection is a critical component of egg survival and is important to the female.

The presence of bright blue color is thus a reliable signal of three things: male quality, breeding status, and dominance. Females respond to this signal, spawning only with blue (sexually mature) males and within that subset, preferring the most intensely colored mate available (Kodric-Brown 1977, 1983). Females, however, use more than just color to identify appropriate mates. When territorial and non-territorial males were moved from lake to laboratory, fed ad libitum for a week, and then matched for size and presented with equivalent territories, females distinguished between the two before they developed full coloration. Males transmitted information about past spawning success via the intensity of their courtship and overall activity, information that was reinforced as their nuptial signal intensified (Kodric-Brown 1995).

Nuptial Color in Sticklebacks: It's Not Just Males

The nuptial male in Stickleback fishes varies from deep black (body, fins, spines, and eye bar: Brook Stickleback, *Culaea inconstans*, McLennan 1993) to a mosaic of red-orange sides, throat and pelvic spine membranes, metallic blue-gray back, and shimmering blue-green eyes (McLennan & McPhail 1989). The function of male nuptial coloration has been so extensively investigated, at least for the Threespine Stickleback (see discussion in McLennan 2006), that for >50 years the courtship interchange appeared to be a monologue; males send, females receive. Nothing could be further from the truth. Threespine Stickleback females become bright gold with a vertical barring pattern along their backs and sides. The intensity of the signal varies within populations; Pacific Coast females are gold all over with light bars, and Lake Ontario and New York females have gold concentrated along the lateral plates and dorsal surface with extremely dark bars (Rowland et al. 1991; DAM pers. obs.). The female nuptial signal in populations of the Brook Stickleback from central and southern Ontario consists of a bright, semi-translucent pink-gold sheen with gold concentrated in the throat and opercular regions and on top of the head, and thin, reticulated, gray bars forming a swirled pattern on the dorsum and sides of the body (McLennan 1994). Once again, differences exist among populations: fish from Nebraska develop darker vertical bars and are less intensely golden than are Ontario fish (Ward & McLennan 2006). Re-examination of previous studies indicated that female nuptial color had been documented but, in a strange kind of Orwellian double think, either ignored or described as cryptic (see photographs of courting female Blackspotted Stickleback, *Gasterosteus wheatlandi*, in McInerney 1969). Overall, intensification of vertical barring occurs in five species: the Threespine Stickleback, Blackspotted Stickleback, Brook Stickleback, Fourspine Stickleback (*Apeletes quadracus*, Rowland 1974; Blouw & Hagen 1981), and Ninespine Stickleback (*Pungitius pungitius*, Morris 1958; McKenzie & Keenleyside 1970).

Sticklebacks respond more to bold than fine checkered patterns (Meesters 1940), so the intensification of vertical barring and swirling seen in the female signal may take advantage of a perceptual or sensory bias in the receiver's (male) visual system. Information transferred by this signal is a reliable indicator of sex and behavioral motivation. In the Threespine Stickleback (Rowland et al. 1991) and Brook Stickleback (McLennan 1994), the origin and the intensity of female nuptial coloration is coupled tightly with ovulation, disappearing rapidly after the female spawns. The signal thus transmits the reliable message that she is a receptive female. Males respond to this message, courting nuptially colored females more intensely than gravid, but cryptically colored, alternatives (Rowland et al. 1991; McLennan 1995). From a male's perspective the ability to differentiate between a courting female and a gravid, but non-ovulated, female provides two benefits. First, the amount of time and energy he invests courting an unreceptive partner is decreased. Second, he can identify potential nest raiders (nonbreeding females, Foster 1990) and egg stealers (neighboring male acting as sneaker). Nest raiding and egg stealing has been documented through direct observation of the phenomenon and implied through discovery of conspecific eggs in stomach analyses for all species of Sticklebacks (FitzGerald 1991). If the fitness of territory holders is generally determined within one season, the potential for nest destruction will be a powerful selection pressure on the male to differentiate between a courting female and threats to his clutch.

The Newest Thing: Ultraviolet Light and Courtship

Ultraviolet-A radiation is composed of short λs (320–400 nm) and is scattered easily by water molecules and solutes (reviewed by Losey et al. 1999). Short wavelengths are also high energy and thus can cause damage to biological systems. Given these two constraints, not surprisingly many biologists assumed that UV radiation was not an important part of courtship communication in fishes. The discovery that many teleosts have retinal pigments that absorb maximally around 360 nm led Macías Garcia & de Perera (2002) to question this assumption, specifically with regards to the courtship of the Darkedged Splitfin (Fig. 2.5), a viviparous toothcarp (Goodeidae) inhabiting shallow, clear waters across the Mexican High Plateau. A male's dorsal and anal fins are edged in black and covered with yellow to orange markings (Fig. 2.5). He displays these fins vigorously during courtship, oriented either laterally to the female or dancing in figure eights in front of her. Females prefer deeper-bodied males, which have larger and more colorful fins (Macías Garcia 1991). Males also perform a seemingly paradoxical courtship display, which involves tucking the dorsal and anal fins to the side away from the female. This action de-emphasizes the fins that first attracted the female, while highlighting the male's dull-silver sides. Under normal laboratory lighting, females pay little attention to this display, but under natural lighting (with UV radiation), a stripe along the male's side and head glows, attracting the female. This attraction disappears when females are used as the stimulus fish.

The UV-based signal thus appears to carry information about sex and possibly species that reinforces the message being transmitted by body shape, fin size, and color. Is this simply a case of redundant coding increasing the probability that the receiver will get the message? Yes and no. The yes is obvious; the UV signal says minimally, "I am a male." No, because UV light is transmitted over such short distances that it likely comes into play only when the courting partners are close together (Fuller 2002). Such short-distance communication may be selectively advantageous because the garter snakes *Thamnophis melanogaster* and *T. eques*, which eat Darkedged Splitfins, can detect UV radiation. The snakes attack both sexes equally, but capture males with larger fins more often, possibly because of the drag resulting from the increased surface area of the erect fins (Fig. 2.5). So, dominant, large-finned males exist in a delicate balance between being preferred by females (benefit) and being more easily captured by predators (cost). When the costs become too high, selection shifts in favor of avoiding predation, so in areas of sympatry with garter snakes, males are slimmer bodied (and smaller finned) than their relatives living without garter snakes (Macías Garcia et al. 1994, 1998). If the flash from the UV stripe attracts the snake to the courting pair, then another cost is added to the balance sheet for dominant, courting males such that males in snake-infested waters should have reduced UV-reflecting areas. On the other hand, if the UV signal is transmitted only over short distances, then no differences should exist in the signal area of similar-sized males from different habitats.

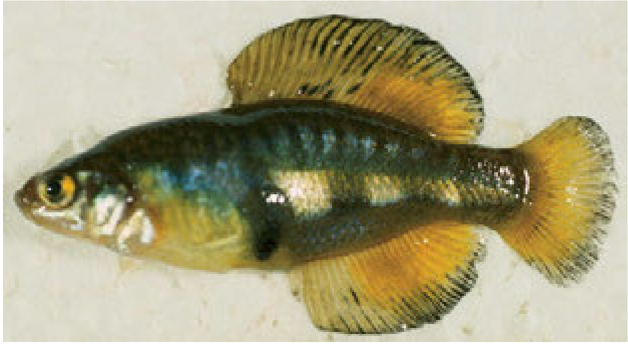

Figure 2.5. Male Darkedged Splitfins, *Girardichthys multiradiatus* (35 mm TL), not only vigorously display their colored dorsal and anal fins during courtship but also tuck those fins away to flash an ultraviolet stripe along their sides and heads. Females, which can detect the flash in natural light (i.e., light with ultraviolet-A radiation), use it to assess males as spawning partners (male, Laguna de Zempoala, Mexico, 16 May 1999; photograph by and used with permission of Shane A. Webb).

UV radiation also plays an important role in swordtail courtship. To our eye, the male sword is a silvery, semitransparent extension on the caudal fin. Under UV light, however, the extensions on the tail of the Panuco Swordtail, Delicate Swordtail, Mountain Swordtail (*Xiphophorus nezahualcoytl*), and Barred Swordtail (*Xiphophorus multilineatus*) (Fig. 2.6), like the Darkedged Splitfin's lateral stripe, flash as the male swims broadside or in a figure eight around the female (Cummings et al. 2003). Interestingly, UV reflectance is not limited to the sword in Panuco

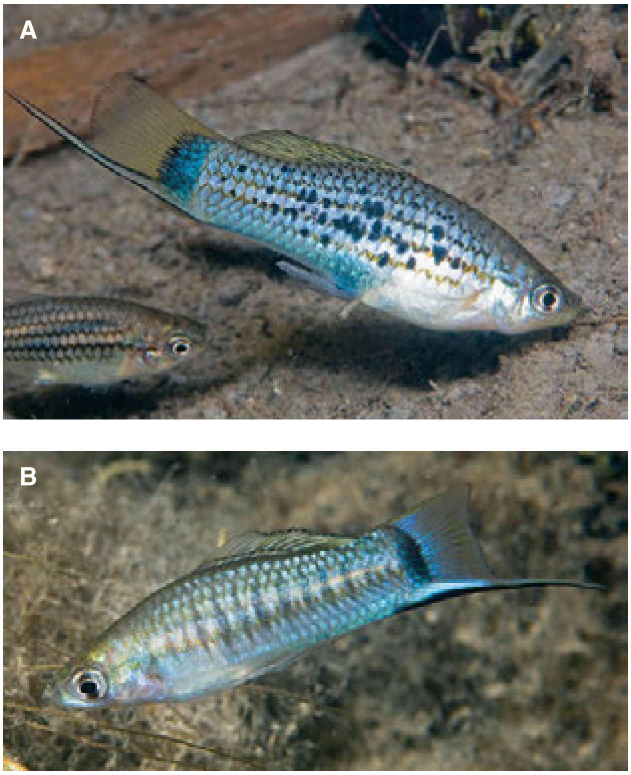

Figure 2.6. Ultraviolet radiation also plays an important role in swordtail courtship. The breeding male's tail extension, which affects the female's perception of his body size (Fig. 2.1), reflects a UV flash as he courts the female (*top*, male Mountain Swordtail, *Xiphophorus nezahualcoytl*, Rio Santa Anita, Rio Panuco drainage, 1 May 2006; *bottom*, male Barred Swordtail, *Xiphophorus multilineatus*, Rio Coy, Rio Panuco drainage, 23 April 2006; photograph by and used with permission of Juan M. Artigas Azas).

Swordtails; it is distributed across the male's body. Large males have more reflective areas on their bodies. Medium males compensate for their UV-challenged status by being more active, engaging in behaviors that enhance the UV flash. For their part, females prefer more active medium males and less active large males. Thus, each type of male possibly adopts the behavioral strategy that will best highlight his UV ornamentation (Cummings et al. 2006).

The discovery of UV-based male traits provided an explanation for the puzzling observation that, unlike females in related species, female Panuco Swordtails do not prefer sworded males; indeed, they showed a trend, albeit insignificant, of being more attracted to swordless males (Rosenthal et al. 2002a). The discovery of the interaction between UV radiation and swords prompted a rerun of the mate choice trials under natural light. When UV light was available, female Panuco Swordtails settled into the plesiomorphic pattern of preferring sworded males (Cummings et al. 2003). So, the initial experiment revealed more about sensory biases introduced into experimental design by human observers than it did about preference in Panuco Swordtails.

Unlike the snake-challenged Darkedged Splitfins, the Panuco Swordtail and the other UV light-reflecting Swordtails contend with predation by Mexican Tetras, which are not sensitive to UV radiation. Such insensitivity provides the swordtails with a private channel for exchanging information: the UV λs reflected from the sword are conspicuous against the background of sidewelling green-yellow light, emphasizing the elaborate trait to conspecifics without attracting the attention of predators. Interestingly, the only species that does not reflect UV radiation from its sword, the Highland Swordtail (*Xiphophorus malinche*), is not sympatric with the Mexican Tetra (Cummings et al. 2003). Presumably the costs of detecting UV radiation (damage to the retina) became an important factor when the benefit of that detection (predator-free communication) was no longer significant.

In summary, the evolution of spectral sensitivity is affected by the transmission properties of the environment (Endler & McLellan 1988) that in turn sets constraints on the parts of the spectrum that are available for building nuptial coloration. Given enough underlying variability in both the receiver and the sender, evolution may eventually produce signal divergence correlated with habitat types or geographical distributions. Few researchers, however, have examined the relationship between receiver response, geographic variability in sender color, and geographic variability in the spectral properties of habitats occupied across the entire range of a species. Ultimately we need these data if we really want to understand the contribution of mating system evolution to the production of freshwater fish diversity. For example, melanic Threespine Sticklebacks tend to be restricted primarily to heavily tannin-stained waters (Reimchen 1989). The general (but not absolute) absence of red males from these habitats makes sense biologically because a signal reflecting photons matching the surrounding spacelight should appear invisible from a distance (McDonald & Hawryshyn 1995; McDonald et al. 1995). In some populations, the change in the male color signal in the novel environment has been matched by a reduction in the female's attraction to red (Boughman 2001). Are we watching speciation in progress? In another example, interpopulation differences in number of speckles on male Jeweled Splitfins, *Xenotoca* *variata*, are not correlated with either habitat clarity or variation in female preference for speckles. In fact, the preference for speckles is only expressed in clear water, implying that females living in turbid habitats may be using non-visual cues to choose mates (Moyaho et al. 2004). Once again, are we documenting speciation in progress? To really attack these and other questions, we need to begin videotaping mate choice trials in murky waters, waters illuminated under low light intensities, or mosaics of light and shadow, in other words, under the range of conditions that has formed the environment of the fish, not the human observer.

SOUND

Sound is a more effective long-distance signal in water than light, electricity, or odor, so it seems intuitive that acoustical cues should play a role in fish communication. This intuition is correct; fishes from >50 families sing to one another in social contexts (Fish & Mowbray 1970; Myrberg 1981). Sound is produced by variations on two general themes (reviewed by Tavolga 1971; Fine et al. 1977; Hawkins 1993): specialized (sonic) muscles insert either directly or via modified skeletal elements on the swim bladder and strike it like a drum (harmonic, low frequency, 40–300 Hz); and processes such as rubbing or grinding bone on bone or snapping tendons over bones produce stridulations (non-harmonic, wide frequency range 100–8,000 Hz). Given that many fishes produce sounds, can they also hear them? Most fishes can detect only low-frequency sounds by direct transmission through the body to the inner ear (≤400 Hz; e.g., Trout-Perch, *Percopsis omiscomaycus*; Ninespine Stickleback; Northern Pike, *Esox lucius*; Spoonhead Sculpin, *Cottus ricei*; Burbot, *Lota lota*; Broad Whitefish, *Coregonus nasus*; Mann et al. 2007). Higher frequencies must be amplified to be transmitted effectively (Hawkins 1993). Amplification is provided by gas-filled structures because gas pulsates when a sound wave passes through it, amplifying and reradiating the sound in all directions. Fishes with the greatest hearing sensitivity (hearing specialists) are characterized by some method for channeling as much of this amplified sound as possible directly to the sacculus (e.g., ostariophysans: the Weberian apparatus, modified vertebrae, found in the Lake Chub, *Couesius plumbeus*, and the Longnose Sucker, *Catostomus catostomus*, can detect sounds from 100 to 1,600 Hz; Mann et al. 2007; Squirrelfishes, Holocentridae: projections from the swim bladder contact the sacculus directly; gouramies, Anabantoidei: the sacculus projects into suprabranchial air chambers; see discussions by Kenyon et al. 1998; Yan et al. 2000). Oddly, many hearing specialists do not produce communicatory sounds, indicating that sound detection and sound production are not necessarily coupled evolutionarily.

The use of sound during courtship creates two problems not encountered with visual cues. First, the ability to detect sound does not require that the receiver be facing the sender (along a line of sight), so the cue is broadcast to many more receivers. Given this public display, selection should favor sounds that are unambiguously species-specific, and if possible, occur outside the detection range of potential predators. Second, frequency, which is an important component of visually based signals, appears to be the least effective component of an acoustical cue because it is extremely sensitive to disturbances in the medium (water) and thus is rapidly degraded. This does not mean that frequency is irrelevant, only that its role is influenced strongly by environmental conditions (e.g., frequency and individual recognition in Elephantfishes, Mormyridae, Marvit & Crawford 2000). Behavioral analyses of song structure and receiver responses indicate that fishes tend to code courtship-based acoustical information in the temporal domain, e.g., the duration, interval between, and repetition rate of the pulses within the sound unit (reviewed by Kihslinger & Klimley 2002). Neurological studies, although rare, complement these observations. The temporal resolution ability of tested fishes falls within the range of other vertebrates and is sufficient for species to detect individual pulses within songs. These capabilities occur in vocal and non-vocal species, indicating that the ability to glean information from pulse duration and interpulse interval predates the appearance of a vocal repertoire. As such, these abilities are properties of the neural-sensory network that collects and processes sound (Wysocki & Ladich 2002).

The focus of most sonic research has been on marine species. Surprisingly little is known about the role of acoustic signals in the breeding systems of North American freshwater fishes. For example, Anderson et al. (2008) dropped a hydrophone into the Hudson River, New York, and discovered a cacophony of sounds, 90% of which were produced between 1500 and 600 h (dusk to dawn). Although they recorded 62 different sounds, they could associate only 4 sounds to fish species, leaving a wide range of purrs, rattles, burps, claps, honks, and drums in the yet-to-be-identified category. Here, I summarize the extent of our knowledge about fishes that sing to each other in fresh waters. The take home message is simple: we may not know much yet, but what we do know is fascinating.

Territorial and Courtship Sounds in Pupfishes

The Cuatro Cienegas Pupfish (*Cyprinodon bifasciatus*) (Fig. 2.7) inhabits relatively shallow, spring-fed pools in Cuatro Cienegas Basin, Coahuila, Mexico. Simultaneous videography and acoustic recordings of territorial males revealed that the majority of sounds a male produced were short (53 ms), low-frequency (391.9 Hz) calls emitted while pursuing an intruder, regardless of the intruder's sex or species. Having dispensed with the intruder, the male returned to patrol his territory and began producing slightly longer (57 ms) and higher-frequency (396.8 Hz) sounds, which continued once a female appeared and he began to follow her. Finally, even longer (61 ms) and higher-frequency (523.4 Hz) calls were occasionally heard immediately after the male and female had spawned. Because of the proximity of the partners, which of the two was producing the post-spawning call was not determined nor was the function of the vocalization (Johnson 2000). The pulses of the Sheepshead Minnow (*Cyrpinodon variegatus*) are the same length and duration as those of the Cuatro Cienegas Pupfish; however, Sheepshead Minnow males often (44.2%) produce a more complex song (≥3 pulses/call) and always sing at a much higher frequency (1,170 Hz versus 408.7 Hz) (Nicoletto & Linscomb 2008). The Sheepshead Minnow hybridizes quite easily with congenerics. Could those mating mistakes be a result, at least in part, of similarities between calls or, alternatively, of differences that might make males of Sheepshead Minnows more attractive to congeneric females (e.g., the increased call complexity)?

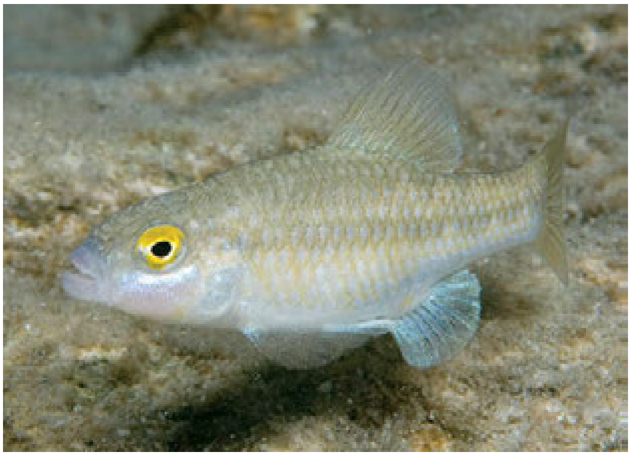

Figure 2.7. Breeding, territorial males of the Cuatro Cienegas Pupfish, *Cyprinodon bifasciatus*, a species endemic to thermal springs of the Cuatro Ciénegas Basin, Coahuila, Mexico, produce short, low-frequency calls while aggressively pursuing conspecific and heterospecific intruders. Calls directed at ovulated females are slightly longer and of higher frequency (male, Poza de la Becerra, Cuatro Ciénegas, 19 November 2006; photograph by and used with permission of Juan M. Artigas Azas).

Do any other cyprinodontiforms call? Unpublished research indicates that the Plains Killifish (*Fundulus zebrinus*), Northern Plains Killifish (*Fundulus kansae*), Golden Topminnow (*Fundulus chrysotus*), Gulf Killifish (*Fundulus grandis*), and Bayou Killifish (*Fundulus pulvereus*) produce low-frequency sounds during courtship (Drewry 1962), and the Bluefin Killifish (Fig. 2.3) emits low-frequency thumps (Foster 1967). Thus calling is possibly more widespread within the larger cyprinodontiform clade than currently is documented.

Territorial and Courtship Sounds in Darters

Male Blackfin Darters (*Etheostoma nigripinne*) and Fringed Darters (*Etheostoma crossopterum*, Fig. 2.8) produce two types of sound, drums and knocks, during the breeding season. Some Blackfin Darter males (27%) add purrs to their repertoire. These three sounds differ in frequency and time- and structure-related parameters: pulse present or absent, pulse number and rate, and call duration. Of the three sound types, drums carry the most intra- and interspecific information. For example, drums are longer compared with knocks in both species; however, Blackfin Darters drum at a higher dominant frequency (138.7 Hz) than do Fringed Darters (89.1 Hz). The shape of the sound

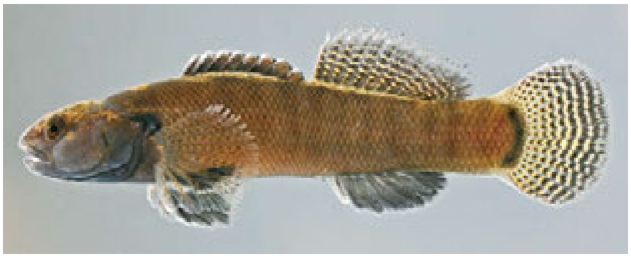

Figure 2.8. Breeding male Fringed Darters, *Etheostoma crossopterum*, produce sounds of two types, drums and knocks. The sounds differ when males are courting females (lower-frequency drums) than when they interact with other breeding males. The mechanism of sound production is unknown; species of *Etheostoma* lack a swim bladder, the site of sound production in many fishes (breeding male, Mill Creek, Union County, Illinois, 19 April 2008; photograph by and used with permission of Uland Thomas).

is context dependent; males from both species produce lower-frequency drums when courting females than when interacting aggressively with conspecific males. Hybrids between the two species produce predominantly drums and do not appear to have any context dependency in their songs. Although the mechanism of sound production is unknown in these darters, they, like other fishes lacking a swim bladder, may produce sounds by the contraction of specialized muscles (Johnston & Johnson 2000a).

Territorial and Courtship Sounds in Minnows

Sound production has been described in seven species of *Cyprinella* (Cyprinidae, Carps and Minnows) (Fig. 2.9A). Satinfin Shiner (*Cyprinella analostana*) males produce sounds during both territorial establishment and courtship (Stout & Winn 1958; Stout 1959, 1960, 1963; Winn & Stout 1960). In the initial stages of territory establishment, competing males produced low-frequency (1,382 Hz), single knocks during lateral threat displays, increasing the frequency of the knocking sounds as the interaction escalated through parallel swim to circle fighting. Territorial males discriminate between an intruding male and female conspecific, reacting to the male with a series of knocks and to the female with spaced, single knocks. Intruders respond to the sounds by moving away, indicating that the sounds serve a threat function. Females always find knocks threatening and will leave the area if they hear them. This may explain why breeding males do not use the more intense form of the signal if a female approaches when she is not ready to breed. The male is possibly warning her to beware, but stay in the area until she is ready to spawn. When a gravid female approaches a courting male, he swims toward her, and awaits her reaction. If she does not flee, he approaches more closely, swims in a circle around her, all fins flared, purring. Purrs are lower frequency (932 Hz) and shorter lived than knocks. A female responds to a purring male by decreasing her activity, thus facilitating the courtship circle display (Stout 1975).

Male Whitetail Shiners (*Cyprinella galactura*), Ocmulgee Shiners (*Cyprinella callisema*), Tricolor Shiners (*Cyprinella trichroistia*; Fig. 2.9A), Tallapoosa Shiners (*Cyprinella gibbsi*), and Edwards Plateau Shiners (*Cyprinella lepida*) also produce distinct sounds during aggressive and courtship interactions. All species produce very low-frequency pulse bursts, Tricolor Shiners and Tallapoosa Shiners chirp and rattle when stationary in front of their crevices, and Ocmulgee Shiners and Whitetail Shiners knock and short knock (Whitetail Shiners only) when aggression escalates from chasing to parallel swimming and lateral displays (Phillips & Johnston 2008a, 2009; Phillips

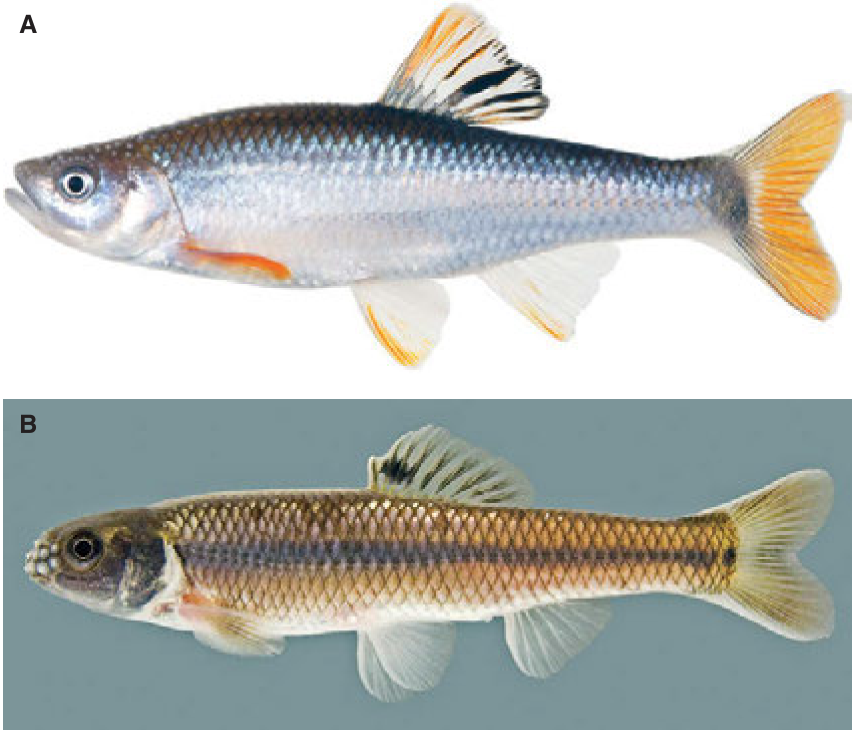

Figure 2.9. (A) In addition to developing head tubercles and displaying bright breeding colors, territorial breeding males of many species of *Cyprinella* (Cyprinidae), like the Tricolor Shiner, *Cyprinella trichroistia*, produce sounds (low-frequency pulse bursts, chirps, and rattles) as they protect their spawning crevices from interlopers and court females. (B) Breeding male Bluntnose Minnows, *Pimephales notatus*, which nest in cavities, do not develop bright colors but they do produce bursts of low-frequency sounds during aggressive encounters with other males; note also the large breeding tubercles on the head (photographs by and used with permission of: Noel M. Burkhead, A, breeding male, Cochran Creek, Dawson County, Georgia, 5 May 2010; Matt Thomas, B, breeding male, Bullskin Creek, Kentucky River drainage, 8 May 2007).

et al. 2010). In general, the rate of calling is more intense at the later stages of agonistic and courtship interactions than at the beginning for all species.

Significant geographical variability exists in pulse parameters (rate, duration, and interval) across populations of Whitetail Shiners in the Ozark and Appalachian Mountains. This variability was organized by distance for courtship-based calls; nonadjacent populations were more divergent than were adjacent ones (Phillips & Johnston 2008b). Low-frequency pulses are often produced by muscles associated with the gas bladder (Demski et al. 1973; Fine et al. 1977). If the underlying mechanism of courtship pulse production, and hence the signal itself, is heritable, then one or more parameters of the call might carry information important to the evolution of assortative mating based on group (population) identity (Phillips & Johnston 2008b). This, in turn, establishes the potential for allopatric speciation, adding freshwater fishes to the long list of avian and anuran species for which an interaction between sound signal variability and geographic location, mate choice, and speciation is known.

The Red Shiner (*Cyprinella lutrensis*) and Blacktail Shiner (*Cyprinella venusta*), also sing, but their songs are not described in the same detail as that of the Satinfin Shiner (Delco 1960; see also courtship knocking sounds in Spotfin Shiner, *Cyprinella spiloptera*, and Pearl Dace, *Margariscus margarita*, Winn & Stout 1960). Both male and female Red Shiners and male Blacktail Shiners could differentiate between conspecific and heterospecific vocalizations. Those vocalizations, however, appeared to be produced only by females, something so unusual that Stout (1975) argued it was an artifact of experimental design. To date, that possibility is untested.

Species of *Cyprinella* are not the only cyprinids to sing during the breeding season. Male Bluntnose Minnows (*Pimephales notatus*; Fig. 2.9B) also produce complex bursts of relatively low-frequency multiple pulses differing in duration and pulse interval (Johnston & Johnson 2000b). These calls are shorter in duration but at about the same dominant frequency as the songs of Ornate Minnows (*Codoma ornata*), which are composed of bursts of low-frequency, non-harmonic pulses. Song length depends on the behavioral context: male-male circle threat (high level of aggression) = male courtship pass over breeding site > male-male lateral threat display > chasing (low level of aggression; Johnston & Vives 2003). Fry raised in isolation from adults (which mirrors the natural situation since Ornate Minnows do not provide any parental care) produced sounds appropriate to the behavioral context, indicating that sound production is innate in this species (Johnston & Buchanan 2007).

Territorial and Courtship Sounds in Sunfishes

Males from at least six species of Sunfishes (Centrarchidae, genus *Lepomis*) grunt or pop during courtship (Gerald 1971). The grunt is a low-frequency sound (<2,000 Hz) that may or may not contain stridulations depending on the species. Mapping these preliminary data onto a phylogenetic tree for the Sunfishes uncovers no discernible pattern in the evolution of grunt stridulations (Fig. 2.10). Such flexibility may indicate that the percent of stridulations within each grunt conveys information that reliably identifies the species of the sender. To this end it is interesting that sister Bluegill (*Lepomis macrochirus*) and Orangespotted (*Lepomis humilis*) Sunfishes show such a strong divergence of percent stridulations, particularly since these two species are almost completely sympatric over their ranges (Lee et al. 1980).

The Pumpkinseed (*Lepomis gibbosus*) and Bluegill make stridulation-like sounds from their pharynxes (called pharyngeal sound production, or PSP), although the details of sound production are unknown. These sounds appear to differ from grunts in both structure (see Fig. 2a in Ballantyne & Colgan 1978a; Fig. 1 in Gerald 1971) and function. Males begin grunting as they approach and swim in courtship circles around a female. PSP occurs immediately following an approach-bite, and appears to signal that the male is in both an aggressive and sexual motivational state. Males increase the number of PSPs/bite when presented with a courting female (Ballantyne & Colgan 1978b) but respond to playbacks of the call with increased levels of aggression regardless of the intruder's sex (Ballantyne & Colgan 1978c). Circumstantially, then, these results indicate that PSP is a male-specific sound used predominantly in aggressive interactions, but it also can be altered to tell an approaching female, "Stay here, I will be ready soon."

More than 30 years of (published) silence have followed the preceding pioneering studies, leaving so much unknown. How are these sounds produced? What factors influenced the loss of singing in the Redbreast Sunfish, *Lepomis auritus* (Fig. 2.10, no sounds detected in 17 courtships and 3 spawnings, Gerald 1971)? What is the function of the calls? Do they convey species-specific information that can be used by females to identify appropriate mates, do they serve to orient and stimulate the female, or both? Preliminary investigations revealed that both male and female

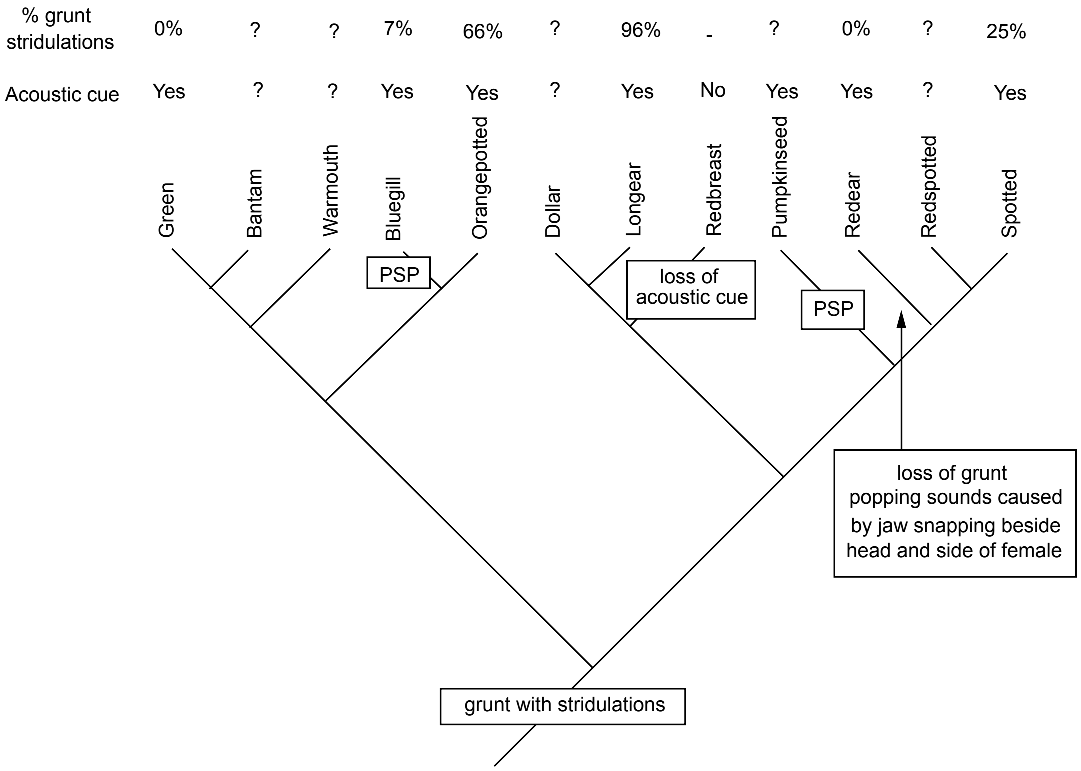
% grunt stridulations
0%
?
?
7%
66%
?
96%
-
?
0%
?
25%
Acoustic cue
Yes
?
?
Yes
Yes
?
Yes
No
Yes
Yes
?
Yes
Green
Bantam
Warmouth
Bluegill
Orangepotted
Dollar
Longear
Redbreast
Pumpkinseed
Redear
Redspotted
Spotted
PSP
loss of acoustic cue
PSP
loss of grunt popping sounds caused by jaw snapping beside head and side of female
grunt with stridulations

Figure 2.10. Presence or absence and details of acoustical cues mapped above a phylogenetic tree for *Lepomis* (Centrarchidae, Sunfishes; Bayesian analysis of three mtDNA and four nuclear genes, Near et al. 2005). The patterns shown are purely heuristic given the lack of detailed cue information and are presented primarily to stimulate further research. PSP = pharyngeal sound production.

Longear Sunfish (*Lepomis megalotis*) and Orangespotted Sunfish were attracted to conspecific over heterospecific calls in field playback experiments (Gerald 1971), and female Pumpkinseeds, but not Longear Sunfish, discriminated between conspecific and heterospecific males in the absence of visual cues (Steele & Keenleyside 1971). Do females call? Overall, questions concerning the role of acoustical cues in mate identification and assessment thus remain (quietly) unanswered for these fishes.

Territorial and Courtship Sounds in Sturgeons

At least eight species of Sturgeon, including six Russian (genus *Acipenser*) and two North American (genus *Scaphirhynchus*) species produce sounds and are attracted to playbacks of their own calls. Both male and female Pallid Sturgeon (*Scaphirhynchus albus*) and Shovelnose Sturgeon (*Scaphirhynchus platorynchus*) squeak (short bursts, relatively high frequency, harmonic), chirp (higher frequency, shorter), knock (low frequency, non-harmonic), and moan (low frequency, non-harmonic) during the breeding season (Johnston & Phillips 2003). Pallid Sturgeons squeaked at a lower dominant frequency with fewer harmonics than Shovelnose Sturgeons, but each squeak lasted almost twice as long. Whether individual sounds were associated with specific contexts could not be determined, suggesting that the low-frequency knocks and moans might be associated with aggregation (low-frequency waves travel farther in water than high-frequency sound), and squeaks and chirps play a role in mate choice once individuals had come together on the spawning grounds. Given the differences between the two species' squeaks, part of the Sturgeon's song also might transmit information about species. What we need to know now is whether the receiver is capable of differentiating between these different messages.

Low-frequency (<500 Hz) sounds attenuate rapidly in the depths used by most spawning North American freshwater fishes because of reflection from the air-water and water-substrate interfaces (Forrest et al. 1993). Thus, the sounds produced by the fishes discussed previously likely function only when individuals are close to one another. These transmission problems decrease the reliability of information transmitted by frequency and suggest that other components of the cue such as temporal patterning—stridulation rate, length of grunt, number of grunts/unit time—should be the focus of selection in many freshwater fish breeding systems (Gerald 1971; Fine et al. 1977). These problems notwithstanding, acoustic cues are an ideal choice for monitoring programs, a less invasive way than trapping to intercept we-are-here messages. Many of the preceding species are on the IUCN (International Union for Conservation of Nature) Red List, so the use of sound to identify and locate their breeding grounds or to stimulate spawning in captive breeding programs is a potentially valuable, and as yet largely untapped, tool for conservation biologists (Luczkovich et al. 1999; Johnston & Phillips, 2003).

OLFACTORY CLUES

Olfactory cues traditionally were classified as long-distance signals in moving water. From a distance, chemical cues may alert the receiver to the presence of the sender before that sender can be located visually. This, in turn, increases the detectability of the visual signal because the receiver is now anticipating a particular event: the appearance of the sender. Unlike visual cues, olfactory cues are transmitted via a turbulent and unpredictable medium, which might lead one intuitively to question whether scent can play anything beyond a general arousal role in courtship. Computer simulations, coupled with experimental manipulations, have revealed, however, that variability in concentration, pulse and interpulse intervals, temporal filter properties of chemoreceptor cells, and the active sampling movements of the receiver can combine to extract temporal, intensity, and directional information from an outwardly chaotic odor plume (Moore & Atema 1988; Jumper & Baird 1991; Moore 1994a).

Odor detection in fishes begins when water enters through the anterior naris and flows over a specialized structure on the floor of the nasal cavity, the olfactory rosette, on its way out of the posterior naris. Olfactory receptors within the rosette are in direct contact with the environment (unlike receptors for electromagnetic and acoustical cues), so processing of olfactory information begins immediately following detection. During the transmission of this information along the sensory cell–olfactory bulb–telencephalon route, about 1,000 sensory cells converge on each secondary neuron, indicating a high degree of sensitivity to chemical cues (see Hara 1986; Hamdanji & Døving 2007).

A role for olfaction in mate and offspring recognition has been demonstrated for a variety of fishes around the world (e.g., Colombo et al. 1982; Burnard et al. 2008). Within North America, researchers have focused their attention on four questions pertaining to mating system evolution. Do males use olfactory cues to discriminate between receptive and nonreceptive females? Can females discriminate between conspecific and heterospecific males based on olfaction alone? Can fishes discriminate kin from non-kin? How do alarm pheromones affect mating behavior?

Do Males Use Olfactory Cues to Discriminate between Receptive and Nonreceptive Females?

Most research concerning male responses to female-based chemical cues has been conducted at the level of the sensory system itself, using electrophysiological responses to different reproductive hormones and their metabolites. Extensive work on the Goldfish, *Carassius auratus*, revealed an elegant two-step system (Fig. 2.11). In the first step, female-released pheromones act as priming agents, altering a male's physiology and preparing him to spawn. The second wave of female pheromones acts as a releaser of male courtship behavior. To date, physiological studies demonstrated that male cyprinids, catostomids, and salmonids are extremely sensitive to F-type prostaglandins, which potentially allows them to distinguish ovulated from unovulated females (Table 2.1). The few studies at the behavioral level for these fishes indicate that physiological responses translate into behavioral realities. Immature Rainbow Trout (*Oncorhynchus mykiss*) treated with 17α-methyltestosterone were attracted to the urine from an ovulated conspecific and preferred her scent to that from a relative (Masu Salmon, *Oncorhynchus masou*, Yambe & Yamazaki 2001b).

Behavioral data alone have confirmed that several male poeciliids can differentiate between receptive and nonreceptive females using olfactory cues (Table 2.1). In poeciliids, ovulation ruptures follicles, releasing estrogen-based steroids bathing the developing ovules, and these steroids drain into the water through the gonopore. A male samples a female's scent by nibbling around her gonopore. This behavior, in conjunction with the demonstration that male Shortfin Mollies (also known in the literature as Atlantic mollies) could identify gravid females with their nares blocked (Zeiske 1968) and studies showing that taste buds are concentrated on the upper side of the head in the Shortfin Molly, Yucatan Molly (*Poecilia velifera*), and Green Swordtail (Fig. 2.1), hints that male recognition of

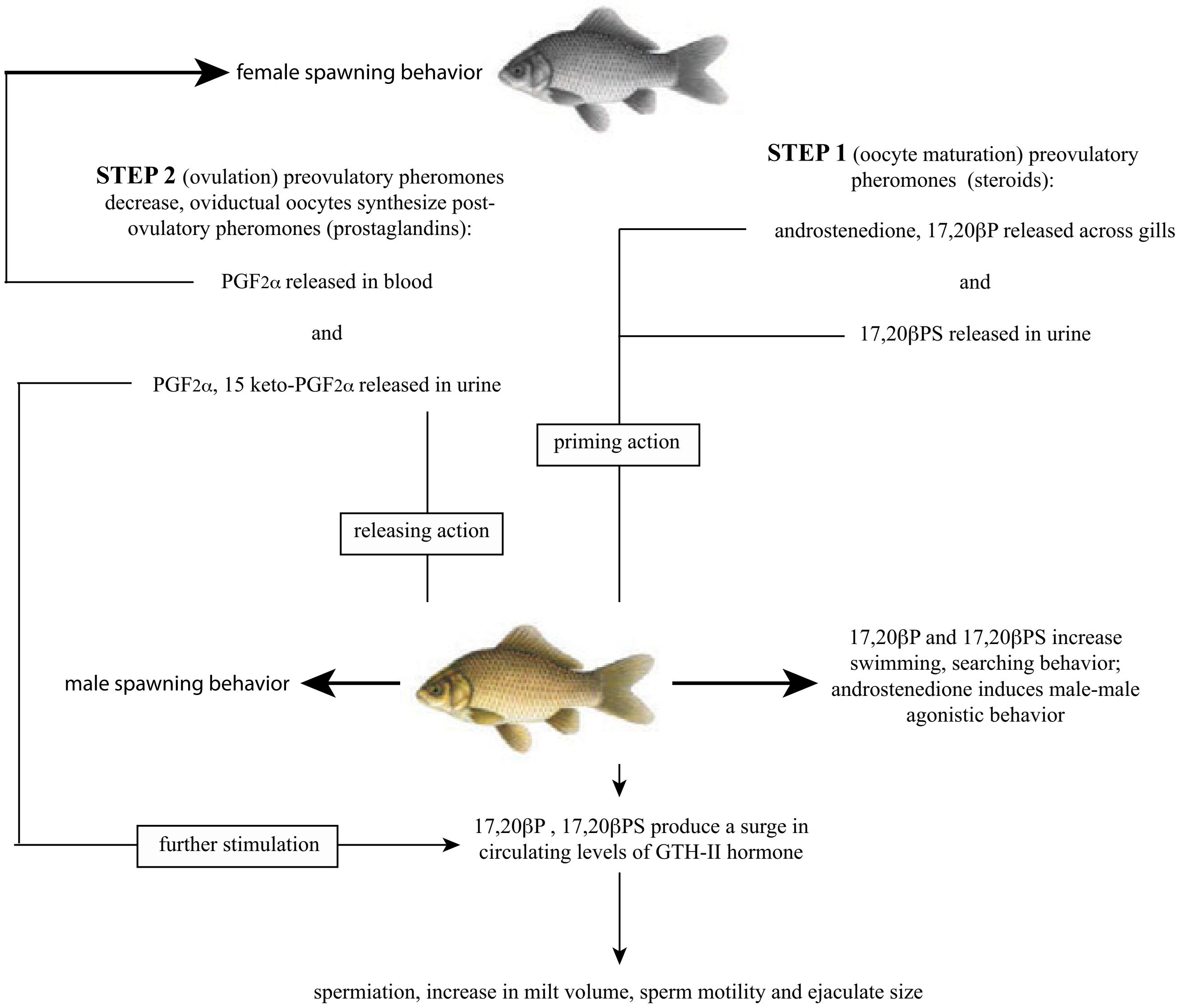
female spawning behavior
STEP 2 (ovulation) preovulatory pheromones decrease, oviductual oocytes synthesize post-ovulatory pheromones (prostaglandins):
PGF2α released in blood
and
PGF2α, 15 keto-PGF2α released in urine
STEP 1 (oocyte maturation) preovulatory pheromones (steroids):
androstenedione, 17,20βP released across gills
and
17,20βPS released in urine
priming action
releasing action
male spawning behavior
17,20βP and 17,20βPS increase swimming, searching behavior; androstenedione induces male-male agonistic behavior
further stimulation
17,20βP , 17,20βPS produce a surge in circulating levels of GTH-II hormone
spermiation, increase in milt volume, sperm motility and ejaculate size

Figure 2.11. Elegant communication system between male and female Goldfish, *Carassius auratus*, based on chemical (olfactory) cues. 17, 20βP = 17α, 20β-dihydroxy-4-pregnen-3-one; $PGF_{2\alpha}$ = Prostaglandin $F_{2\alpha}$ (references in Chung-Davidson et al. 2008; Hoysak & Stacey 2008; color and black-and-white insets by and used with permission of Joe Tomelleri).

female receptivity in poeciliids may be gustatory rather than olfactory. The mechanism is different from that recorded for cyprinids (Fig. 2.11), but the function, female fertility or receptivity advertisement, is the same. Females may benefit from such advertisement by decreasing the amount of male harassment outside their receptive period and by inciting competition among various suitors during their fertile period (Park & Propper 2002). These benefits are not bought at a high cost since the cues are byproducts of ovary development and ovulation and thus relatively cheap to use.

The ability to discriminate between females at different stages of their ovulatory cycle may itself be coupled with male reproductive strategy. For example, large male Sailfin Mollies (Fig. 2.2) distinguish between the two female conditions (ovulating and non-ovulating), directing most of their courtship efforts toward females that are more likely to respond positively (Sumner et al. 1994; see also Broadspotted Molly, *Poecilia latipunctata*, Ptacek et al. 2005). Small Sailfin Molly males, on the other hand, are not choosey and will attempt to mate with a female regardless of her receptivity. Such wasted courtship effort may be offset by the fact that small males attempt more copulations overall than do large ones (see alternative mating strategies section).

To this point I have examined the influence of a female-based scent cue on male physiology and behavior.

Table 2.1. Sexual pheromones in North American freshwater fishes. Unless otherwise stated, the source of the olfactory cues is water in which individuals were previously held.

Species	Sexual Olfactory Cues (sex of sender-sex of receiver)	References
Anguillidae (Freshwater Eels)		
Anguilla rostrata (American Eel)	*Female-male*: increased swimming activity.	Sorenson & Winn 1984
Petromyzontidae (Lampreys)		
Petromyzon marinus (Sea Lamprey)	*Male-female* (and bile acids or synthetic 3kPZS): increased swimming activity, search behavior, and attraction; attraction increases with concentration of cue in simultaneous encounters; main component is 7α, 12α, 24-trihydroxy-3-one-5α-cholan-24-sulfate (3kPZS) possibly released across gills; can discriminate between bile acids released by conspecific adult males and larvae. Pre-ovulating females did not respond. *Male-male* (spermiating, pre-spermiating males): no response. *Female-female* (ovulatory, pre-ovulatory females): no response. *Male-male* (spermiating, pre-spermiating males): no response. *Female-female* (ovulatory, pre-ovulatory females): no response.	Teeter 1980; Bjerselius et al. 1996; Li et al. 2002, 2003ab; Yun et al. 2002, 2003; Siefkes et al. 2003ab, 2005; Siefkes & Li 2004; Johnson et al. 2005, 2006a; Li 2005; Wagner et al. 2006
Clupeidae (Herrings)		
Dorosoma petenense (Threadfin Shad)	*Adult-adult* (+ mucus): no response.	McMahon & Tash 1979
Characidae (Characins)		
Astyanax sp.	*Female-male*: attracted to scent.	Wilkens 1971
Cyprinidae (Carps and Minnows)		
Pimephales promelas (Fathead Minnow)	*Male-female*: attracted to scent. *Female-female*: attracted to scent.	Cole & Smith 1987, 1992
Catostomidae (Suckers)		
Catostomus catostomus (Longnose Sucker)	*Female-male*: males sensitive to PGF-2α but further data needed to determine whether this acts as a sex pheromone; cannot distinguish between conspecific and White Sucker.	Cardwell et al. 1992
Catostomus commersoni (White Sucker)	*Female-male*: PGF-2α increased GtH levels in males; cannot distinguish between conspecific and Longnose Sucker.	Stacey et al. 1984; Cardwell et al. 1992
Ictaluridae (North American Catfishes)		
Ameiurus melas (Black Bullhead)	*Both* substrate mark (urine and/or mucus): attracted to scent. *Male-female* (in lab and field): attracted to scent.	Liley 1982 and references therein; Kendle 1970; Wallace 1970
Ictalurus punctatus (Channel Catfish)	*Female-male*: attracted to scent. *Male-female*: attracted to scent.	Liley 1982 and references therein; Timms & Kleerekoper 1972
Salmonidae (Trouts and Salmons)		
Coregonus clupeaformis (Lake Whitefish)	*Female-male and female*: both increased swimming activity in response to synthetic PGF-2α and metabolites; most sensitive to 15-keto-PGF2α and 13, 14-dihydro-PGF2α.	Hara & Zhang 1998; Laberge & Hara 2003ab
Oncorhynchus mykiss (Rainbow Trout)	*Female-male*: preferred scent from ovulated to non-ovulated female; ovarian fluid increased males' courtship; released in urine; raises levels of 17α, 20β-dihydroxy-4-pregnen-3-one, testosterone, GtH II, and milt levels in males (in some experiments). Not sensitive to F-type prostaglandins. Preferred scent of conspecific to Masu Salmon (*Oncorhynchus masou*) *Male-female*: attracted to scent. *Both* (spawning pair): attracted to scent.	Liley 1982 and references therein; Newcombe & Hartman 1973; Emanuel & Dodson 1979; Honda 1980; Sveinsson & Hara 1990; Olsén & Liley 1993; Scott et al. 1994; Vermeirssen et al. 1997; Hara & Zhang 1998; Sato & Suzuki 2001; Vermeirssen & Scott 2001; Yambe 2001; Yambe & Yamazaki 2001ab; Laberge & Hara 2003b
Oncorhynchus nerka (Sockeye Salmon)	*Female-male* (urine): attracted to scent.	Liley et al. 1993

Table 2.1, continued

Species	Sexual Olfactory Cues (sex of sender-sex of receiver)	References
Salmo salar (Atlantic Salmon)	*Female-male* (ovarian fluid-urine): scent from both conspecific and *Salmo trutta* raises levels of 17α, 20β-dihydroxy-4-pregnen-3-one, 11-KT, T, and also increased milt volume. Cue is a PGF. *Juvenile-juvenile* (kin or non-kin): preference based on sharing MHC class II alleles. Analysis of spawning pairs indicated that individuals choose a partner different from themselves based on MHC complement (cannot tell whether this pattern is female- or male-based, or both).	Moore & Scott 1992; Moore & Waring 1996a; Waring et al. 1996; Hara & Zhang 1998; Olsén et al. 2000, 2001, 2002b; Landry et al. 2001; Rajakaruna et al. 2006
Salmo trutta (Brown Trout)	*Female-male and female* (ovarian fluid-urine): scent from both conspecific and Atlantic Salmon raises levels of 17α, 20β-dihydroxy-4-pregnen-3-one in males; response <Atlantic Salmon. Both sexes increased swimming activity in response to synthetic PGF-2α and 13, 14-dihydro-PGF2α; trend for females to increase levels of nest digging and probing. Copper(II) sulfate or the pesticide cypermethrin in water reduces response in males.	Essington & Sorensen 1996; Hara & Zhang 1998; Olsén et al. 1998a, 2000; Moore et al. 2002; Laberge & Hara 2003b; Jaensson et al. 2007; Jaensson & Olsén, 2010
Salvelinus alpinus (Arctic Charr)	*Male-female*: release PGF-2α; attracts female, stimulates digging behavior. *Juvenile-juvenile* (kin or non-kin): preference based on sharing MHC class II alleles, although unidentified genes (possibly MHC class I) also were implicated. Did not differentiate between dominant/subordinate individuals, but did prefer scent from siblings who had eaten a similar diet. No study yet showing whether this influences future mate choice.	Sveinsson & Hara 1990, 1995ab, 2000; Olsén et al. 1998b, 2002a, 2003
Salvelinus fontinalis (Brook Trout)	*Female-male*: males sensitive to PGF-2α and metabolites. *Juvenile-juvenile* (kin or non-kin): preference based on sharing MHC class II alleles.	Essington & Sorensen 1996; Rajakaruna et al. 2006
Gasterosteidae (Sticklebacks)		
Culaea inconstans (Brook Stickleback)	*Male-female*: recognized conspecific and Threespine Stickleback; preferred conspecific. *Female-male*: recognized conspecific and Threespine Stickleback but was not attracted to the heterospecific; preferred conspecific. Discriminated between scent of conspecific females and males.	McLennan 2003, 2004, 2005
Gasterosteus aculeatus (Threespine Stickleback)	*Male-female*: more attracted to water from displaying than non-displaying male, or to a male with a nest than a male without one. More attracted to olfactory cues than visual cues in eutrophic waters; acidification (as in eutrophic waters) enhanced olfaction. Preferred a conspecific male whose MHC class IIB genotype in combination with her own genotype optimized the diversity of MHC alleles in her offspring; spent more time with the scent of a male rather than a female conspecific, regardless of the MHC allele genotype of either stimulus fish. The MHC signal alone was not enough to attract a female, indicating that the reproductive pheromone is more than just MHC, possibly androgen-based. Preferred scent from unrelated male versus a brother. Recognized conspecific and Brook Stickleback cues; preferred conspecific. Benthic females more attracted to the scent of benthic versus limnetic males; limnetic females show no choice. *Male-male*: more attracted to water from displaying than non-displaying male. Males did not differentiate between water from a brother versus an unrelated male (in terms of aggression directed toward computer images accompanied by the different scents).	Waas & Colgan 1992; Reusch et al. 2001; Aeschlimann et al. 2003; McLennan 2003; Milinski 2003; Häberli & Aeschlimann 2004; Milinski et al. 2005; Frommen & Bakker 2006; Rafferty & Boughman 2006; Heuschele & Candolin 2007; Mehlis et al. 2008; Sommerfeld et al. 2008; Eizaguirre et al. 2009; Heuschele et al. 2009; Lenz et al. 2009; Mehlis et al. 2009

(continued)

Table 2.1, continued

Species	Sexual Olfactory Cues (sex of sender-sex of receiver)	References
Centrarchidae (Sunfishes)		
Lepomis macrochirus (Bluegill Sunfish)	*Male-male*: scent of adult males delayed maturation in juvenile males.	Aday et al. 2003, 2006
Cyprinodontidae (Pupfishes)		
Cyprinodon beltrani (Blackfin Pupfish)	*Male-female*: attracted to scent of conspecific males versus water, but did not discriminate between conspecific males and Thicklip Pupfish or Maya Pupfish. *Female-female*: did not discriminate between female cue and water.	Strecker & Kodric-Brown 1999
Cyprinodon labiosus (Thicklip Pupfish)	*Male-female*: preferred conspecific over Blackfin Pupfish and Thicklip Pupfish.	Strecker & Kodric-Brown 1999; Kodric-Brown & Strecker 2001
Cyprinodon maya (Maya Pupfish)	*Male-female*: preferred conspecific over Blackfin Pupfish and Thicklip Pupfish.	Strecker & Kodric-Brown 1999; Kodric-Brown & Strecker 2001
Cyprinodon pecosensis (Pecos Pupfish)	*Male-female*: do not differentiate between conspecific and water.	Rosenfield & Kodric-Brown 2003
Cyprinodon variegatus (Sheepshead Minnow)	*Male-female*: do not differentiate between conspecific and water.	Rosenfield & Kodric-Brown 2003
Poeciliidae (Livebearers)		
Gambusia affinis (Western Mosquitofish)	*Female-male* (receptive-nonreceptive): males attracted to odor from all reproductive stages but only increased copulation attempts to receptive female odor.	Park & Propper 2002
Poecilia chica (Dwarf Molly)	*Female-male* (receptive-nonreceptive): 1 day after parturition (increased male-male interactions, copulation attempts).	Hilton & Grosse 1981; Brett & Grosse 1982
Poecilia latipinna (Sailfin Molly)	*Female-male* (receptive-nonreceptive female): requires contact (gonopodial nibbling); large, but not small, males differentiate between females. Did not differentiate between cues from conspecific females versus gynogens (Atlantic Mollies, *Poecilia formosa*).	Liley 1982 and references therein; Sumner et al. 1994; Aspbury et al. 2010a
Poecilia mexicana (Shortfin Molly, cave population)	*Female-male*: were not attracted; males able to identify gravid females with nares blocked; taste buds on body surface, concentrated on dorsal surface of the head.	Parzefall 2001
Xiphophorus birchmanni (Sheepshead Swordtail)	*Male-female*: preferred conspecific scent to that of Highland Swordtail (*X. malinche*) except when tested in stream water with elevated levels of humic acid (no preference); more attracted to scent from well-fed versus food-deprived males. Preferred scent of conspecific males to that of Variable Platyfish in areas of syntopy but did not differentiate in areas with few Variable Platyfish. Did not distinguish between the scent of males from their own versus an allopatric population. *Female-male*: attracted to scent of conspecific and Highland Swordtail but not Variable Platyfish; preferred the conspecific when matched against Variable Platyfish, but preferred Highland Swordtail over the conspecifics. *Female-female*: do not discriminate between well-fed and food-deprived females. *Fry-adults*: attracted to scent, possibly because it conveys information about nutritional state (presence of food). Perhaps this could be later co-opted in mate choice.	Wong et al. 2005; Coleman & Rosenthal 2006; Fisher & Rosenthal 2006; Fisher et al. 2006; Fisher & Rosenthal 2010
Xiphophorus cortezi (Delicate Swordtail)	*Male-female*: attracted to scent from conspecific, Panuco and Montezuma Swordtails. Preferred conspecific over other two species.	McLennan & Ryan 1997

Table 2.1, continued

Species	Sexual Olfactory Cues (sex of sender-sex of receiver)	References
Xiphophorus montezumae (Montezuma Swordtail)	*Male-female*: attracted to scent from conspecific, Panuco and Delicate Swordtails. Prefers conspecific over Panuco Swordtail; does not discriminate between conspecific and Delicate Swordtail.	McLennan & Ryan 1999
Xiphophorus nigrensis (Panuco Swordtail)	*Male-female*: attracted to scent from conspecific and Delicate Swordtail, but does not respond to Montezuma Swordtail. Prefers conspecific over other two species and over Pygmy Swordtail.	Crapon de Caprona & Ryan 1990; McLennan & Ryan 1999
Xiphophorus pygmaeus (Pygmy Swordtail)	*Male-female*: did not discriminate between conspecific and Panuco Swordtail; preferred scent of conspecific to Delicate Swordtail.	Crapon de Caprona & Ryan 1990; Hankison & Morris 2003
Xiphophorus variatus (Variable Platyfish)	*Male-female*: Preferred scent of conspecific males to that of sympatric Sheepshead Swordtail in areas of overlap. Did not distinguish between the conspecific and scent of Sheepshead Swordtail from an allopatric population.	Fisher & Rosenthal 2010
Gobiidae (Gobies)		
Neogobius melanostomus (Round Goby, a Great Lakes invasive species)	*Male-female*: ovulated female attracted (but not to water from non-reproductive males), increased activity, increased olfactory epithelial activity; non-gravid females are not attracted but do swim more. Gravid females attracted to 5α-androstan-3α-ol-17-one-3-glucuronide source, may even oviposit. Pheromone in urine. Holding water did not increase attraction to models of nuptially colored males. *Female-male*: do not respond by changing activity levels, orientation, or location. *Female-female*: non-reproductive females attracted (but not ovulated females). *Male-male*: do not respond. *Electro-olfactogram*: males and females detected free and conjugated 18-, 19-, and 21-carbon steroids, but not prostaglandins. Estrone, 17beta-estradiol-3beta-glucuronide, or etiocholanolone increased ventilation rate in males, etiocholanolone, increased ventilation rate in females.	Colombo et al. 1982; Murphy et al. 2001; Zielinski et al. 2003; Belanger et al. 2004; Gammon et al. 2005; Corkum et al. 2008; Marentette & Corkum 2008; Kereliuk et al. 2009; Yavno & Corkum 2010
Percidae (Perches)		
Gymnocephalus cernuus (Ruffe, a Great Lakes invasive species)	*Female-male*: increased swimming only in response to odor of females immediately prior to ovulation. Cue might be 4-pregnen-17, 20β, 21-triol-3-one.	Sorensen et al. 2004

Female-female interactions have not been studied in nearly the same detail. Two studies highlight the kind of unexpected information that may be gathered when researchers think outside the box (or aquarium). Exposing male and female Western Mosquitofish fry to the scent from two males, two females, or one male and one female produced only one significant result: female fry grew more slowly, had smaller ovaries, and were more likely to die when exposed to the odor from just two adult females (Lutnesky & Adkins 2003). Maintaining wild-caught adults under similar sex-biased regimes produced complementary results: females in the female-biased treatment grew less and produced fewer offspring than their sisters in male-biased or balanced sex ratio pools. No differences occurred in the levels of female aggression across the three treatments, refuting the hypothesis of behavioral suppression and implicating the influence of a chemical cue (Smith & Sargent 2006).

Can Females Discriminate between Conspecific and Heterospecific Males Based on Olfaction Alone?

Researchers interested in female responses to male-based chemical cues tend to approach the problem from a behavioral angle (Table 2.1). For example, although Sticklebacks have a small olfactory epithelium (only two folds in each nasal rosette, Teichmann 1959), female Threespine Sticklebacks and Brook Sticklebacks are capable of discriminating between the scent of conspecific and heterospecific males, even though they are attracted to the heterospecific (McLennan 2003). A female's response to the male scent changes across her ovulatory cycle in the same way that her reaction to male nuptial coloration changes. She is attracted to the male scent immediately following ovulation, then within 24 h of spawning, she moves away from the odor. Both visual and olfactory cues are thus reinforcing the male's message of courtship readiness, allowing the female to approach or avoid him depending on her own internal state (McLennan 2005).

The situation is more complicated in swordtails, in which female response to male cues is influenced by phylogenetic distance and male type. So, I begin with the female's response to male scent in three species (Montezuma Swordtail, *Xiphophorus montezumae*, Delicate Swordtail, and Panuco Swordtail) with large, courting males. Phylogenetically, Montezuma Swordtails are basal to a clade comprising the Delicate Swordtail + Panuco Swordtail (Rauchenberger et al. 1990; Meyer et al. 1994). In mate recognition trials, female Delicate Swordtails and Montezuma Swordtails found the scent of all heterospecific males attractive. Delicate Swordtails were particularly entranced by the odor from closely related Panuco Swordtail males. Female Panuco Swordtails were attracted to olfactory cues from Delicate Swordtails but did not respond to cues from the more distantly related Montezuma Swordtails (asymmetry #1). In mate discrimination trials, Panuco Swordtail and Delicate Swordtail females strongly preferred their own males. Montezuma Swordtail females, on the other hand, only demonstrated a strong preference for the conspecific stimulus when it was matched against the most distantly related Panuco Swordtail (asymmetry #2). The asymmetries in attraction and discrimination imply that, minimally, the Delicate Swordtail and Panuco Swordtail share an apomorphic change in some aspect of their olfactory cue–receiver system that is not shared with Montezuma Swordtails. Interestingly the Montezuma Swordtail, the most basal of the three, is least capable of discriminating between conspecific and heterospecific cues. Similar results occurred for morphospecies in a Pupfish species flock in Mexico (Strecker & Kodric-Brown 1999).

Although intuitively pleasing, the story, like so much in evolution, is not so simple; female response to the message in the male-based olfactory cue is influenced by factors other than phylogenetic distance in some species. Female Panuco Swordtails preferred the scent of their own large, courting males to the scent of the Pygmy Swordtail (*Xiphophorus pygmaeus*, this species contains only small sneaker males). The reverse comparison was not significant; female Pygmy Swordtails did not discriminate between conspecific and heterospecific males (Crapon de Caprona & Ryan 1990). Does the asymmetry reflect the retention of a preference in Pygmy Swordtail females for the scent of large, courting males? Preliminary data from another species with only small, sneaker males, the Short-sword Platyfish, *Xiphophorus continens*, support this suggestion; female Short-sword Platyfishes actually prefer the scent from large, courting male Montezuma Swordtails (a close relative) to the scent of their own males (McLennan & Ryan 2008).

Male-based olfactory cues act as physiological primers, stimulating ovulation in maturing females (Chien 1973; Chen & Martinich 1975; van den Hurk & Lambert 1983; van den Hurk et al. 1987; van Weerd et al. 1988; Resink et al. 1989b) and helping to synchronize the courtship dialogue (Dulka et al. 1987; Bjerselius et al. 1995 and references therein). Olfactory cues also clearly provide some species-specific information and are thus a cohesive component (Brooks & Wiley 1988) of the mate recognition system (sensu Paterson 1985) in some fishes. Male-based sexual pheromones generally are composed of conjugated and free steroid metabolites, prostaglandins, or both (Resink et al. 1989a; Lambert & Resink 1991; Becker et al. 1992; Cardwell et al. 1992; Kitamura et al. 1994; Sorensen & Scott 1994 and references therein; Sveinsson & Hara 1995ab; Robison et al. 1998). The level of the stimulatory effect of these substances depends on their structure and their relative concentrations, implying that detailed and species-specific information may be transmitted by a multicomponent olfactory cue (syntactic coding, Colombo et al. 1982; Lambert et al. 1986; Resink et al. 1989a; Sorensen et al. 1995a). Detection of these pheromones is associated with the medial olfactory tract (MOT) in teleosts. The MOT innervates, among other things, areas of the telencephalon and preoptic area that affect GtH (gonadotrophin) production, which in turn regulates reproductive physiology and behavior (see Kyle et al. 1987; Resink et al. 1989c; Laberge & Hara 2001 and references therein). Whatever the mechanism, the preceding studies indicate that olfactory cues also contain a conservative component that can confound mating decisions.

The male-based olfactory cue also may transmit information about an individual's allelic complement of major histocompatibility complex (MHC) genes (part of the immune system). For example, several hundred different alleles were identified in Threespine Stickleback populations (at six class II MHC loci), which translates into extremely high polymorphism at the population level. The number of MHC alleles/individual is normally distributed in wild populations with the greatest number of individuals showing an intermediate number (Reusch et al. 2001; Wegner et al. 2003ab). Fish with intermediate numbers of MHC alleles, in turn, show lower susceptibility to parasitic infection (Wegner et al. 2003ab, 2006; Kurtz et al. 2004), increased survivorship (Wegner et al. 2008), and higher lifetime reproductive success (Kalbe et al. 2009), so an intermediate number of MHC alleles is apparently optimal for Threespine Sticklebacks. Choice trials demonstrated that a female extracts information from scent about a potential suitor's allelic complement, and from that chooses a male who, in combination with her own genotype, produces offspring with the optimal (intermediate) number of MHC alleles (Reusch et al. 2001; Aeschlimann et al. 2003; Milinski et al. 2005; Eizaguirre et al. 2009; Lenz et al. 2009). Just how a female knows her genotype remains unknown, although perhaps she extracts information from her own scent; nor has the component of the male-based cue that carries the information about MHC genotype been identified.

Can Fishes Discriminate Kin from Non-Kin?

A few freshwater fishes, mainly salmonids, can differentiate between kin and non-kin based on olfactory cues (Coho Salmon, *Oncorhynchus kisutch*, Quinn & Busack 1985; Quinn & Tolson 1986; Rainbow Trout, Brown & Brown 1992, 1993b, Brown et al. 1993; Atlantic Salmon, *Salmo salar*, Stabell 1982, 1987; Brown & Brown 1992; Moore et al. 1994; see also Fathead Minnow, Brown & Smith 1994). Arctic Charr, *Salvelinus alpinus*, are capable of this type of discrimination following the development of a recognition template based on the MHC class II B, exon 2 locus, another closely linked MHC loci transmitted in olfactory cues, or both. The template is formed during social interactions at a critical period early in life (Selset & Døving 1980; Olsén 1989, 1992; Winberg & Olsén 1992; Olsén & Winberg 1996). When individual fish are presented with two different scents, they compare each scent to their template and move toward the one with the best fit (phenotypic matching, Waldman 1987). The template is extremely sensitive and highly polymorphic; fish preferred MHC-identical siblings to MHC-disparate siblings, and MHC-disparate siblings to nonsibling-MHC genotypes (Olsén et al. 1998). There are two potential benefits to this recognition. First, kin who shoal together generally weigh more than individuals in non-kin groups (in the laboratory anyway). This difference in body weight could be partly due to the increased aggressive behavior non-kin group members direct to one another and increased energy cost of defending larger territories (Brown & Brown 1993ab, 1996; Brown et al. 1996; Olsén et al. 1996). The second benefit occurs later in life when, presumably, the kin recognition template is used to actively reject siblings as potential mates. At the moment, MHC-based disassortative mating has been demonstrated only in mice (Potts et al. 1991), but if such a system is operating in this and other species of fishes, like the Sticklebacks discussed previously, it could be one way to avoid inbreeding and maintain genetic diversity.

Taken together, these results imply a fair amount of olfactory flexibility in fishes. Unlike visual and auditory systems, the olfactory system is a shallow (cortical interpretation is only two neurons away from receptors), low-bandwidth sense that appears to favor global perception rather than precise segmentation (Laurent 1999). Global perception implies that responses to particular scents are not hard-wired; rather, the structure of the neurological system permits associative learning, linking scents with a variety of objects, including home stream, individual conspecifics, prey items, and predators (Olsén 1992; Valentincic et al. 1994). Behavioral flexibility is an important component in complex social systems, but it comes at a price. For example, in most of the species (Table 2.1) the heterospecific cue conveys meaningful information to the breeding female. Thus, a potential for females to make mating mistakes can occur based solely on olfactory information.

Alarm Substance and Breeding

The Ostariophysi are renowned for possessing specialized epidermal cells, which produce and release Schreckstoff (fright substance) when damaged (von Frisch 1938, 1941; Pfeiffer 1962, 1963a; reviewed in R. J. F. Smith 1992). When conspecifics detect the cue, they respond with species-specific anti-predator behaviors. For example, Fathead Minnows (Mathis & Smith 1993a) increase their tendency to shoal, darters freeze (R. J. F. Smith 1979), and Green Sunfish (*Lepomis cyanellus*) decrease movement and increase dorsal fin erection (Brown & Brennan 2000). At one time, Schreckstoff was thought to be a unique synapomorphy for the Ostariophysi, but recent research has uncovered alarm pheromones in a wide variety of non-ostariophysan fishes, including salmonids, cottids, centrarchids, gasterosteids, poeciliids, and percids (Table 2.2). Given this wide taxonomic diversity, it is unlikely that alarm pheromones arose only once in the history of the Ray-finned Fishes (Actinopterygii) or that the pheromone is the same in each group, although some overlap apparently exists. For example, cyprinids respond to skin extract from gasterosteids (Chivers & Smith 1994c) but not from salmonids (Pfeiffer 1963b). Within major groups, almost all of the species that respond to skin extract from conspecifics also respond to extract from distantly related heterospecifics, indicating that the signal itself must contain an evolutionarily conservative component. The nitrogen oxide functional group is the prime molecular trigger in the ostariophysan alarm cue. Hypothetically, the trigger could be coupled with various molecules, including hypoxanthine-3-N-oxide, to produce an array of alarm signals within the clade (G. E. Brown et al. 2000). This combination of evolutionarily conservative and flexible signal components produces the pattern by now familiar to researchers studying alarm cues: cyprinids and darters react to skin extracts from members of their own clade but never as intensely as they react to conspecific extract, and they do not respond equally to all heterospecifics.

From a mating perspective, the presence of alarm pheromones presents a special problem for fishes whose mating behaviors involve abrasive activities like scraping or rubbing against rocks or sticks during nest building or courtship because inadvertent release of the substance would tend to send presumptive partners fleeing in different directions. Little research is available on this problem, despite the fact that R. J. F. Smith (1973) called attention to it >40 years ago. The majority of species respond to the presence of alarm substance with reduced activity (Table 2.2). Even fishes that dart or scatter do not appear to go far before stopping and remaining quiet. All other things being equal, then, mates will not move far away from one another, if at all, in response to the accidental release of the pheromone. Does this mean that the problem is a trivial one? The answer to this question, as Smith anticipated, is an overwhelming no. Courtship has been interrupted, wasting valuable time and energy and increasing the likelihood that one of the partners will break off the interaction.

This problem can be circumvented in at least two ways. First, a change in the production of the olfactory cue can occur (modifications in the message, change in the sender). This happens in several cyprinid species in which increasing androgen levels are correlated with the disappearance of alarm substance–producing cells of males and occasionally females (Smith 1973, 1974, 1976a, 1978; Smith & Murphy 1974). A change in the sender is not necessarily coupled with a corresponding change in the receiver. For example, male Fathead Minnows lose the ability to produce alarm substance during the breeding season, but they retain their fright reaction to it (remember, they respond to cues from relatives) as do females (Smith 1976b). In fact, males will decrease territorial activity and even go as far as abandoning their nests if exposed to alarm pheromone or the scent of a minnow-fed predator (Jones & Paszkowski 1997). Thus, males possibly use the intensity of such olfactory cues to adjust their reproductive behavior and to choose nesting sites that are as predator-free as possible.

The correlation between loss of alarm production and abrasive behavior is not a perfect one (Table 2.2), bringing us to the second possibility: changes may occur in the detection or response to the message (change in the receiver). The reaction of Eurasian Minnows (*Phoxinus phoxinus*) to Schreckstoff was far less intense (feeding rate decreased and shoal size increased only slightly) and more transitory when they were tested in a fluvarium built into a riverine side channel versus in the laboratory (Irving & Magurran 1997; see also Magurran et al. 1996; Wisenden et al. 2004). This suggests that response to Schreckstoff is context dependent in the field; individuals may increase their vigilance slightly but in the absence of any visual cues from an approaching predator, continue with their normal activities. Similar responses occur with food-deprived darters (R. J. F. Smith 1981), Fathead Minnows (Brown & Smith 1996), and Reticulate Sculpins (*Cottus perplexus*) (Chivers et al. 2000). The context-dependent nature of the alarm response may explain why some fishes that produce alarm substance and have abrasive courtship do not fly apart, freeze, or otherwise lose contact with one another during breeding. The situation is, however, more complex because the context is partially established by characteristics of the breeding habitat. Species breeding in shallow, slow-moving waters or in confined places under rocks and branches might be expected to be affected more strongly by the inadvertent release of alarm cues during courtship than species breeding in the open or in fast-moving waters. The clarity of the water may be important as well; alarm behavior in the laboratory is more

Table 2.2. Alarm signaling in North American freshwater fishes (N/A, not applicable; ?, unknown).

Species	Alarm Signaling (response to conspecific skin extract)[1]	Abrasive Courtship	Seasonal Loss of Alarm Cells	References
Cyprinidae (Carps and Minnows)				
Campostoma anomalum (Central Stoneroller)	YES	YES	YES (male and female)	Smith 1976a
Chrosomus eos (Northern Redbelly Dace)	YES, and to Brook Stickleback and Fathead Minnow. Moved closer to substrate, dashing, freezing, increased school cohesion; avoided areas marked with cue. Response affected by concentration of cue. Acts synergistically with visual cues; increases shoaling behavior.	?	?	Wisenden et al. 2003; Dupuch et al. 2004; Wisenden & Barbour 2005; Wisenden 2008
Chrosomus neogaeus (Finescale Dace)	YES, and to Fathead Minnow, less intensely to Brook Stickleback and synthesized hydroxylamine and pyridine-N-oxide. Increased shoaling, avoidance in the field.	YES	~YES: fewer cells both sexes	Stasiak 1978; Smith & Smith 1983; Chivers & Smith 1994c, 1998; G. E. Brown et al. 2000, 2001a; Friesen & Chivers 2006
Chrosomus erythrogaster (Southern Redbelly Dace)	YES	?	?	Verheijen 1963
Couesius plumbeus (Lake Chub)	YES, slightly less strongly to Redside Shiner, Peamouth, and Longnose Dace.	NO	NO	Pfeiffer 1963b; Smith 1976a
Cyprinella lutrensis (Red Shiner)	YES	?	?	Smith & Smith 1983
Cyprinella spiloptera (Spotfin Shiner)	YES	?	?	Verheijen 1963
Cyprinella venusta (Blacktail Shiner)	YES	YES	YES (male)	Reed 1969; Pflieger 1975; Pfeiffer 1977; Smith & Smith 1983
Cyprinella whipplei (Steelcolor Shiner)	YES	YES	YES (male)	Pflieger 1965; Smith & Smith 1983
Hybognathus hankinsoni (Brassy Minnow)	YES	?	?	Pfeiffer 1963a
Luxilus cornutus (Common Shiner)	YES, sought cover if predator perceived to be a bird.	YES	YES (male)	Smith 1976a; Heczko & Seghers 1981
Mylocheilus caurinus (Peamouth)	YES, slightly less strongly to Northern Pikeminnow and Longnose Dace.	?	?	Pfeiffer 1963b
Nocomis biguttatus (Hornyhead Chub)	YES	YES	YES (male)	Smith 1976a
Notropis heterolepis (Blacknose Shiner)	YES, fewer fish in the area after alarm cue released; intensified avoidance of model trout.	?	?	Wisenden et al. 2004
Pimephales notatus (Bluntnose Minnow)	YES	YES	YES (male)	Smith 1976a
Pimephales promelas (Fathead Minnow)	YES, and to Brook Stickleback, Northern Redbelly Dace, Finescale Dace, Iowa Darter, and synthesized hydroxylamine. Increased use of shelter, dashing, freezing, and shoal cohesion; avoided areas marked with cue; synergistic interaction between alarm cue and visual cues increases shoaling	YES	YES (male)	Smith 1973, 1974, 1976b; Smith & Murphy 1974; Levesley & Magurran 1988; Lawrence & Smith 1989; Mathis & Smith 1992, 1993bcde; Mathis et al. 1993, 1996; Chivers & Smith 1994abc, 1995,

(*continued*)

Table 2.2, continued

Species	Alarm Signaling (response to conspecific skin extract)[1]	Abrasive Courtship	Seasonal Loss of Alarm Cells	References
	behavior; strongest response to conspecific cue with next strongest response to guild member (Brook Stickleback). Learns to respond to heterospecific alarm cue, dependent on the density of Brook Sticklebacks and complexity of the habitat (did not learn in habitats with complex structure or a low density of Brook Sticklebacks). Small individuals respond to alarm cue from damselfly larvae (share many predators). Degree of alarm cell development related to condition of individual fish. Learned predator recognition: alarm cue is excreted by predator (Northern Pike, Yellow Perch, Brook Trout) when it eats a minnow, coupling the alarm scent with the predator's scent. Learned to associate a novel sound cue and red light with the scent of the alarm substance. Response declines with age of extract and is correlated with intensity of cue concentration.			1998; G. E. Brown et al. 1995ab, 1997, 2000, 2001b; Chivers et al. 1995abc, 2002; Wisenden et al. 1995b, 2003, 2008b, 2009a; Brown & Smith 1996; Irving & Magurran 1997; Wisenden & Smith 1997; Yunker et al. 1999; Mirza & Chivers 2001a, 2003cd; Gazdewich & Chivers 2002; Pollock & Chivers 2003, 2004; Pollock et al. 2003, 2006; Ferrari et al. 2005, 2006; Wisenden & Barbour 2005; Ferrari & Chivers 2006; Friesen & Chivers 2006; Wisenden 2008
Pimephales vigilax (Bullhead Minnow)	YES	YES	YES (male)	Smith 1976a
Ptychocheilus lucius (Colorado Pikeminnow)	YES. Reduced movement, seeking cover, agitation, dashing.	?	?	Beyers & Farmer 2001
Ptychocheilus oregonensis (Northern Pikeminnow)	YES, slightly less strongly to Redside Shiner, Peamouth, Lake Chub, Longnose Dace, and Longnose Sucker; does not respond to Coho Salmon (*Oncorhynchus kisutch*).	?	?	Pfeiffer 1963b
Rhinichthys cataractae (Longnose Dace)	YES, less strongly to Northern Pikeminnow, Redside Shiner, Peamouth, Lake Chub, and Longnose Sucker; does not respond to Coho Salmon.	NO	NO	Pfeiffer 1963b; Smith 1976a
Richardsonius balteatus (Redside Shiner)	YES, less strongly to Northern Pikeminnow, Peamouth, Longnose Dace, and Longnose Sucker; does not respond to Coho Salmon.	?	?	Pfeiffer 1963b
Semotilus atromaculatus (Creek Chub)	YES	YES	YES (substantially reduced in male, but not female)	Smith 1976a
Semotilus margarita (Pearl Dace)	YES. Rapid scattering then freezing.	NO	YES (male, dramatically reduced in female)	Smith 1976a; Rehnberg et al. 1987
Catostomidae (Suckers)				
Catostomus catostomus (Longnose Sucker)	YES, less strongly to Redside Shiner and Peamouth; no response to Coho Salmon.	?	?	Pfeiffer 1963b

Table 2.2, continued

Species	Alarm Signaling (response to conspecific skin extract)[1]	Abrasive Courtship	Seasonal Loss of Alarm Cells	References
Catostomus commersoni (White Sucker)	YES	NO	YES (male)	Smith 1976a
Catostomus macrocheilus (Largescale Sucker)	YES, less strongly to Peamouth.	?	?	Pfeiffer 1963b
Characidae (Characins)				
Astyanax bimaculatus (Twospot Astyanax)	YES, and to Banded Astyanax.	?	?	Pfeiffer 1963a
Astyanax fasciatus (Banded Astyanax)	YES, epigean populations. Rapid, zigzag swimming, hiding, avoidance of water surface. YES, cave populations. Avoid water surface.	?	?	Pfeiffer 1963a; Thinès & LeGrain 1973; Fricke 1987
Astyanax mexicana (Mexican Tetra)	Alarm cells present (also in cave populations) but no behavioral studies done.			Peters et al. 1990
Ictaluridae (North American Catfishes)				
Ameiurus natalis (Yellow Bullhead)	YES	?	?	Todd et al. 1967
Ameiurus nebulosus (Brown Bullhead)	YES	?	?	Pfeiffer 1963ab
Ictalurus punctatus (Channel Catfish)	YES, and to extract from Sunfish spp. Alarm cells identified in epidermis. Increased activity, time spent motionless. Identified as hypoxanthine-3-*N*-oxide (hydroxylamine).	?	?	Pfeiffer 1977; Yoakim & Grizzle 1982; Chapman & Johnson 1997; Brown et al. 2003
Salmonidae (Trouts and Salmons)				
Salmo salar (Atlantic Salmon)	YES. Decreased activity, number of feeding attempts; increased time near substrate and hiding. Learned novel odor recognition. Took longer to resume foraging after exposure to a novel visual stimulus if exposed to alarm cues first.	YES	?	Leduc et al. 2006, 2007ab; Kim et al. 2009
Salmo trutta (Brown Trout)	YES, and to Brook Trout and Rainbow Trout. Decreased activity.	YES	YES	Mirza & Chivers 2001b
Salvelinus fontinalis (Brook Trout)	YES, and to Brown Trout. Decreased activity, moved to shelter, increased shoaling, decreased foraging. Small Brook Trout responded more strongly to cues from small individuals than to cues from large individuals and vice versa. Disturbance[2] signal (released prior to capture): reduce movement. Learned predator recognition: respond to cues from Yellow Perch or Northern Pike that have eaten conspecifics or Rainbow Trout but not Brook Stickleback.	YES	YES	Mirza & Chivers 2000, 2001b, 2002, 2003a; Leduc et al. 2004
Oncorhynchus mykiss (Rainbow Trout)	YES, and to Brook Trout and Brown Trout. Decreased activity, increased time in shelter, lower in water column. Interesting suggestion that infection with *Diplostomum cercariae* released	YES	?	Brown & Smith 1997, 1998; Poulin et al. 1999; Mirza & Chivers 2001b, 2003b; Brown et al. 2003; Scott et al. 2003; Leduc

(continued)

Table 2.2, continued

Species	Alarm Signaling (response to conspecific skin extract)[1]	Abrasive Courtship	Seasonal Loss of Alarm Cells	References
	alarm cues. Does not respond to hydroxylamine. Learned predator recognition. Dominant and subordinate individuals differ in response depending on whether they are alone and on food ration. Disturbance[3] signal (released prior to capture): decreased activity.			et al. 2004, 2008; Scheurer et al. 2007; Smith et al. 2008; Brown et al. 2009; Vavrek & Brown 2009
Oncorhynchus tshawytscha (Chinook Salmon)	YES. Stop swimming, stop feeding, sink to bottom. Learned predator recognition.	YES	?	Berejikian et al. 1999
Esociformes (Pikes)				
Esox lucius (Northern Pike)	NO	N/A	N/A	Schutz 1956
Umbra limi (Central Mudminnow)	YES. In the field: traps caught fewer individuals. In the lab: reduction in activity, movement to the bottom.	?	NO, not detected	Wisenden et al. 2008a
Fundulidae (Topminnows)				
Fundulus olivaceus (Blackspotted Topminnow)	YES?	NO	?	Cited as having alarm cues in Cashner 2004, but no reference given
Poeciliidae (Livebearers)				
Gambusia affinis (Western Mosquitofish)	YES. Freeze at top of water or swim to substrate.	NO	?	Reed 1969; Bryant 1987; García et al. 1992
Xiphophorus helleri (Green Swordtail)	YES, more weakly to Guppy (*Poecilia reticulata*) but did not respond to Fathead Minnow. Males reduce activity near top of water, females moved to bottom and shelter.	NO	?	Mirza et al. 2001
Cottidae (Sculpins)				
Cottus cognatus (Slimy Sculpin)	YES. Increased shelter use. Disturbance signal: decreased number of short moves.	?	?	Bryer et al. 2001
Cottus perplexus (Reticulate Sculpin)	YES. No response to Speckled Dace (*Rhinichthys osculus*). Decreased movement.	?	?	Chivers et al. 2000
Myoxocephalus scorpius (Shorthorn Sculpin)	YES	?	?	Pfeiffer 1960
Gasterosteidae (Sticklebacks)				
Culaea inconstans (Brook Stickleback)	YES, and more weakly to Fathead Minnow. Increased shoaling; move downward in water; decreased activity if alone; synergistic interaction between alarm cue and visual cues increases shoaling behavior.	?	?	Mathis & Smith 1993a; Chivers & Smith 1994c, 1998; Wisenden et al. 1994, 1995b, 2003; Friesen & Chivers 2006; Wisenden 2008
Gasterosteus aculeatus (Threespine Stickleback)	YES, and more weakly to *Apeltes quadracus* (Fourspine Stickleback).	?	?	Brown & Godin 1997
Centrarchidae (Sunfishes)				
Enneacanthus chaetodon (Blackbanded Sunfish)[3]	NO	N/A	N/A	Pfeiffer 1977

Table 2.2, continued

Species	**Alarm Signaling (response to conspecific skin extract)**^{1}	**Abrasive Courtship**	**Seasonal Loss of Alarm Cells**	**References**
Lepomis cyanellus (Green Sunfish)	YES, and to Finescale Dace and synthetic hydroxylamine. Decreased movement; erected dorsal spines when small, but increased approach, spines prone in response to Dace cue when large (ontogenetic shift).	?	?	Brown & Brennan 2000; Golub & Brown 2003
Lepomis gibbosus (Pumpkinseed)	YES (regardless of size and habitat complexity), and to Green Sunfish and synthetic hydroxylamine. Juveniles show decreased movement, erected dorsal spines, more sensitive to cue concentration. Ontogenetic shift in response to alarm cue from Largemouth Bass: in low and medium habitat complexity small and medium-sized individuals showed anti-predator response, large individuals continued foraging. In high habitat complexity, all size classes showed anti-predator reaction. Did not react to cues from Fathead Minnow.	?	?	Leduc et al. 2003; Marcus & Brown 2003; Wisenden et al. 2003; Golub et al. 2005
Micropterus punctulatus (Spotted Bass)	NO response to skin extracts from Blacktail Shiner, Bullhead Minnow, Western Mosquitofish, Blackspotted Topminnow, or Bluegill (*Lepomis macrochirus*).	N/A	N/A	Cashner 2004
Micropterus salmoides (Largemouth Bass)	YES, and to Finescale Dace and Green Sunfish, but only when juveniles (ontogenetic shift). Decreased movement; moved to substrate, away from cue.	?	?	Brown et al. 2001b, 2002b
Percidae (Perches)				
Ammocrypta beanii (Naked Sand Darter)	YES, and to Blackbanded Darter, only weakly to Gulf Darter. Reduced activity, no rapid darts.	?	?	Smith 1982
Etheostoma caeruleum (Rainbow Darter)	YES, and to Yoke Darter (*Nothonotus juliae*), Banded Darter (*Etheostoma zonale*), Redfin Darter, Fathead Minnow, but not to Greenside Darter (*Etheostoma blennioides*), Fantail Darter, or *Brachygobius doriae*. Reduced activity, increased opercular beat rate.	?	?	Commens & Mathis 1999; Gibson & Mathis 2006; Commens-Carson & Mathis 2007
Etheostoma exile (Iowa Darter)	YES, but did not respond to Johnny Darter (but dosage low). Increased dashes, then reduced activity; assumed head-up, swayback posture. Avoided traps treated with alarm cue in the field. Evidence of a disturbance signal:[3] increased head-up vigilance.	?	?	R. J. F. Smith 1979, 1981; Wisenden et al. 1995a; McPherson et al. 2004
Etheostoma flabellare (Fantail Darter)	NO, and did not respond to Rainbow Darter or Redfin Darter.	N/A	N/A	Commens-Carson & Mathis 2007

(continued)

Table 2.2, continued

Species	Alarm Signaling (response to conspecific skin extract)[1]	Abrasive Courtship	Seasonal Loss of Alarm Cells	References
Etheostoma nigrum (Johnny Darter)	YES, and to Slenderhead Darter (*Percina phoxocephala*) but not to Orangethroat Darter, Logperch, or Blackside Darter (*Percina maculata*) Freeze, then reduced activity; assume head-up, swayback posture; response present in lab-reared individuals.	?	?	R. J. F. Smith 1979; Haney et al. 2001; Vokoun & Noltie 2002
Etheostoma spectabile (Orangethroat Darter)	YES, and to Johnny Darter, Logperch, Slenderhead Darter, but not to Blackside Darter. Reduced activity.	?	?	Carmichael cited in R. J. F. Smith 1981; Haney et al. 2001
Etheostoma swaini (Gulf Darter)	YES, and to Naked Sand Darter and Blackbanded Darter. Rapid darts followed by reduced activity.	?	?	Smith 1982
Etheostoma whipplei (Redfin Darter)	YES, and to Rainbow Darter but not Fantail Darter.	?	?	Commens-Carson & Mathis 2007
Percina caprodes (Logperch)	NO, and did not respond to Orangethroat Darter, Johnny Darter, Slenderhead Darter, or Blackside Darter.	N/A	N/A	Haney et al. 2001
Percina nigrofasciata (Blackbanded Darter)	YES, and to Naked Sand Darter and Gulf Darter. Reduced activity, few rapid darts, cryptic coloration.	?	?	Smith 1982
Perca flavescens (Yellow Perch)	YES, and to Iowa Darter and Spottail Shiner (*Notropis hudsonius*). Ontogenetic shift in response to conspecific and heterospecific cues. Increased use of shelter, stationary. Olfactory processing disrupted by heavy metal contamination.	?	?	Mirza et al. 2003, 2009; Harvey & Brown 2004

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[1] Studies demonstrating that predators are attracted to the alarm cues of their prey were not included in this table because presumably this interaction would never result in a mistaken heterospecific mating.

[2] Some animals release disturbance chemicals when they are frightened but not injured. Ammonia, released in the urine or across the gills, serves this function in amphibians and crustaceans; source is unknown in fishes (Bryer et al. 2001).

[3] Pfeiffer (1977) based this on the absence of specialized epidermal club cells; however, other centrarchids that were also scored as "No" (e.g., Pumpkinseed) are now known to produce and respond to alarm substances. This species thus needs to be reinvestigated.

intense in turbid than in clear water (Hartman & Abrahams 2000).

One other question is relevant to the release of alarm substances as a side effect of breeding: How do predators respond to the presence of Schreckstoff? If they are attracted to alarm signals, then the cost of accidentally releasing these chemicals during abrasive courtship increases. The answer to this question is equivocal. Northern Pike are attracted to the alarm scent from Fathead Minnows in the lab (although that result may be an artifact of experimental design; Cashner 2004), as are a variety of unidentified piscivores in the field (Wisenden & Thiel 2002), but Spotted Bass (*Micropterus punctulatus*) do not react to skin extracts from Blacktail Shiners (*Cyprinella venusta*), Bullhead Minnows (*Pimephales vigilax*), Blackspotted Topminnows (*Fundulus olivaceus*), Western Mosquitofish, or Bluegills, all of which co-occur with the predator. For the moment, the best explanation is that selection for predator recognition of prey alarm signals is dependent on how predators handle their prey, which in turn sets the boundaries on a predator's ability to associate the scent of a prey's alarm substance with the presence of that prey (e.g., pike tend to mouth their prey, bass do not, Cashner 2004). Overall, then, the relationship between alarm cues and breeding will be affected by variables of the breeding habitat, the presence or absence of abrasive courtship, and changes in the cue production, receiver response, or both. Unfortunately, in the 40 years since Smith alerted us to the paradoxical relationship between alarm cues and (potentially) abrasive courtship, few researchers have attempted to solve the paradox.

Perhaps more than any other modality, the presence of chemical cues used in mate recognition, and responses by receivers to those cues, challenges our concept of signal. Release of such cues is often a byproduct of physiological processes. For example, as discussed previously, in poeciliids ovulation ruptures follicles, releasing the estrogen-based steroids bathing the developing ovules, and these steroids drain through the gonopore. Males are capable of responding to these steroids, so it is obvious that the cue transmits information. This begs the question, is the female signaling her receptivity? If the definition of signal is something that causes a change in behavior "because of information content rather than physical force, and (which has been) specifically altered by selection in some way to achieve that end" (Guilford & Dawkins 1992:384), then the female cue is not a signal unless selection has altered the specific components of the steroidal soup associated with ovulation to enhance its signal value (Liley 1982). It is, nonetheless, an important component of the communication system between male and female. It might even be an example of the initiation of a sensory bias process; in this case, something in the male's sensory system is biased toward the detection of female-based steroids. What we may be seeing is the beginning of signal evolution, combining Gould and Vrba's (1982) concept of exaptation (the cue) with Ryan's concept of sensory bias (perception and response by the receiver), which may in time lead to a modification of the cue to enhance its role in communication, thus, producing a true signal.

PUTTING IT ALL TOGETHER

Something is intriguing about animals that live in caves, perhaps because their sensory environment is so completely foreign to us. Consider, e.g., fish living in Cueva del Azufre near Tapijulapa in Tabasco, Mexico (Gordon & Rosen 1962). Water running through the cave is saturated with toxic hydrogen sulfide and low in oxygen, but it appears to be energy-rich based on deposits of bat guano and chemoautotrophic production by sulfide-oxidizing bacteria. In these extreme conditions, a troglobitic population of Shortfin Mollies (Fig. 2.12) can be found (Parzefall 1993; Langecker et al. 1996). Epigean Shortfin Mollies have the familiar poeciliid breeding system: alternative male mating strategies (small sneaker males and large, brightly colored but non-courting males, Parzefall 1969; Plath et al. 2007a), females subjected to high levels of male harassment (Plath et al. 2003a, 2004a, 2007a), male-male competition with the advantage going to larger males, and female preference for large males (Bisazza & Pilastro 1997; Plath et al. 2004b, 2007b). How has this system changed in the perpetual deep night at the back of the cave? The most obvious change has been a dramatic simplification of male-male aggressive behavior. Notably, displays that involve visual signaling or the need for rapid coordinated movements (fin erection, tail lifting, s-threat, ramming, biting, and circling) are dropped from the repertoire, leaving only tail beating (Parzefall et al. 1997). Water displaced by this display, which is performed at close range between the two antagonists, is detected by the hyper-developed lateral-line system (Parzefall 1970). Changes to the lateral line also were implicated in the

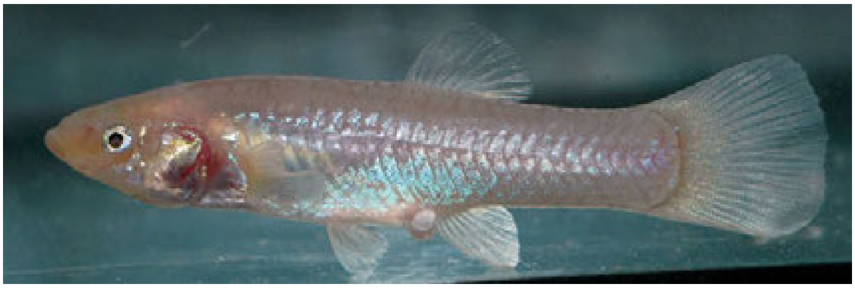

Figure 2.12. Relative to epigean populations, the cave-dwelling populations of the Shortfin Molly, *Poecilia mexicana* (female, shown here), have a hyper-developed lateral-line system, an increased number of olfactory and taste receptors, and simplified courtship behaviors. Males use olfaction and taste to determine receptivity of females, in part by nibbling around the female's gonopore. Note the enlarged genital pad of the female, which presumably is involved in production or dispersal of reproductive chemical cues (female, Chamber X, Cueva del Azufre, near Tapijulapa, Tabasco, Mexico, October 2010; photograph by and used with permission of Michael Tobler).

ability of cave females, unlike their epigean relatives, to differentiate between small and large males in complete darkness (Körner et al. 1999; Plath et al. 2003c, 2004b, hydrodynamic imaging sensu Hassan 1989 for cave-dwelling Banded Astyanax, *Astyanax fasciatus*). Cave females have a second derived characteristic: they are capable of discriminating between well-fed and starved males using visual and/or olfactory cues. They appear to fall on one end of an evolutionary trajectory from no choice (epigean females in energy-rich habitat) to choice based on visual cues alone (epigean females in energy-poor environment; putative close relatives of cave population) to choice based on both visual and chemical cues (troglobitic females in energy-rich but high-density environment) (Plath et al. 2005).

As mentioned previously, male Shortfin Mollies do not court, so there are no visual displays to modify in this environment. More interestingly, males of all sizes appear to use only one strategy in the cave: find a female, attempt to mate with her. Why the loss of alternative mating strategies? Male Shortfin Mollies in the cave show an overall reduction in general reproductive behaviors, including aggression, sexual activity, and female harassment (Parzefall 1974, 1979; Parzefall et al. 1997; Plath et al. 2003a, 2004a, 2007a). Such a damping down of male behavior may reflect the need to divert energy to solve two general problems. First, although the cave environment has been described as energy-rich, cave mollies are generally not in good condition (Plath et al. 2005; Tobler et al. 2006). They are constantly expending energy detoxifying hydrogen sulfide and swimming to the surface to breathe. They thus exist in a precarious state in which they must have a constant supply of energy-rich food to stave off starvation (Plath et al. 2007c). Given this stress, energetically expensive male behavioral displays have not surprisingly been either lost or reduced in the cave population. One side effect of this reduction in sexual behavior is that males no longer spend as much time chasing and harassing females, attempting to force copulations. The benefits, in terms of energy savings, to the male are obvious. Interestingly, this change also benefits the female. In epigean livebearers, females must spend time and energy watching for, and fleeing from, harassing males (Plath et al. 2003a, 2007a; see also Plath 2008 and references therein). Such a loss of feeding time would be disastrous in the cave, but the reduction in levels of male harassment allows females to spend more time feeding when males are present (Plath et al. 2007a).

The second energy-based problem involves the costs of searching for a mate, which intuitively should be higher for males living in dark, extreme environment. So, just how do males find a mate? This has proven to be a difficult question to answer. Males do not distinguish between males and females from a distance based on any type of sensory input (Plath et al. 2001; Plath et al. 2003b), nor do they respond to the scent of a female (Zeiske 1968). Once a female is located, however, a male can identify her receptive state by using the plesiomorphic behavior of nibbling around her gonopore. Cave-born females have a large, extensively folded genital pad containing numerous mucous cells, which presumably are involved in the production or dispersal of chemical cues. This structure is not prominent in epigean females. Taste buds scattered all over the surface of the fish, particularly on the upper side of the head, can detect such cues, and fish from the farthest part of the cave (receiver) have more taste organs on their body surface compared with epigean stock and close relatives. Gustation is thus likely an important sensory modality in these fish (Parzefall 1970, 2001). Overall then, the visual, chemical (both gustation and olfaction), and near touch components of the mating dialogue in epigean Shortfin Mollies have undergone compensatory modifications in the deep cave populations, changing the structure of the sensory hierarchy. Most of those changes involved a simplification of male reproductive behaviors and mating strategies. Females, on the other hand, show a derived ability to identify the nutritional status of males based on chemical cues, while retaining the plesiomorphic preference for large males. They just use a different sensory system(s) to identify their favored partner.

Since I first began to work on this chapter another population of Shortfin Mollies was discovered in a cave (Cueva Luna Azufre), near Tapijulapa, Tabasco, Mexico (Pisarowicz 2005). The water in Luna Azufre is only slightly acidic, and therefore does not support a thriving population of bacterial chemoautotrophs, so the major food source is bat guano. Not surprisingly, Shortfin Mollies from this cave are malnourished (Tobler et al. 2007). This discovery is exciting (perhaps not so much for the mollies) because it gives us the opportunity to test the hypothesis that extreme energy limitation in Cueva del Azufre was causally involved in modifying the behavior of cave dwellers. The hypothesis was indeed supported by observations on fish in the new cave. As predicted, males showed reduced sexual behavior and levels of harassment, and male presence did not affect female feeding rate (Plath 2008).

LOVE AT LAST: THE IMPORTANCE OF EGGS

Egg Stealing and Alloparental Care

Alloparental care means caring for unrelated offspring. In fishes, this usually involves a male taking over a nest that already contains eggs, stealing eggs and placing them in his own nest, or being unable to prevent cuckolders or other species from spawning in his nest. Alloparental care via egg stealing and nest takeover occurs in numerous North American freshwater fishes, all of which have a polygamous, male-only parental care breeding system (Table 2.3). How can such behavior be maintained if the name of the evolutionary game is getting your genes into the next generation? A critical component to the breeding success of polygamous, paternal males seems to be acquiring their first clutch because females generally prefer to mate with males who already have eggs in their nest (e.g., Threespine Stickleback, Ridley & Rechten 1981; Jamieson & Colgan 1989, 1992; Goldschmidt et al. 1993; Kraak & Groothius 1994; Fathead Minnow, Page & Swofford 1984; Unger & Sargent 1988; Tessellated Darter, *Etheostoma olmstedi*, Constanz 1979, 1985; Unger & Sargent 1988; Fantail Darter, *Etheostoma flabellare*, Knapp & Sargent 1989; Page & Bart 1989). The expression of this preference will depend on factors such as the way in which eggs are deposited in the nest (clumped versus laid in a single layer) and thus may be flexible under some circumstances. For example, female Common Gobies (*Pomatoschistus microps*) reverse their preference for guarding males in oxygen-stressed water, a condition under which massed eggs have a more difficult time receiving an adequate oxygen supply even with male fanning (Reynolds & Jones 1999). Overall, though, female preference for egg-guarding males creates the selection arena favoring the evolution of egg stealing by males.

So, why should females display a preference for nests with many eggs? Four hypotheses have been proposed to answer this question. First, a female's eggs are less likely to be eaten by a predator, a guarding male, or a nest raider if they are placed within a larger cluster of unrelated eggs (the dilution effect, Rohwer 1978; Ridley & Rechten 1981; Unger & Sargent 1988; Jamieson & Colgan

Table 2.3. Alloparental care in North American freshwater fishes.

Species	References
Cyprinidae (Carps and Minnows)	
Pimephales promelas (Fathead Minnow)	Unger & Sargent 1988; Sargent 1989
Gasterosteidae (Sticklebacks)	
Gasterosteus aculeatus (Threespine Stickleback)	Wootton 1971; Li & Owings 1978ab; Rohwer 1978; Belle-Isles et al. 1990; Goldschmidt & Bakker 1990; Goldschmidt et al. 1992, 1993; Jamieson & Colgan 1992; Rico et al. 1992; de Fraipont et al. 1993; Mori 1995ab; Largiadér et al. 2001
Cottidae (Sculpins)	
Cottus paulus (Pygmy Sculpin)	Johnston 2000a
Centrarchidae (Sunfishes)	
Lepomis auritus (Redbreast Sunfish)	DeWoody et al. 1998
Lepomis cyanellus (Green Sunfish)	Hunter 1963
Lepomis gibbosus (Pumpkinseed)	Rios-Cardenas & Webster 2005
Lepomis marginatus (Dollar Sunfish)	MacKiewicz et al. 2002
Lepomis macrochirus (Bluegill)	Neff 2001
Lepomis megalotis (Longear Sunfish)	Jennings & Philipp 1992, 2002
Lepomis peltastes (Northern Longear Sunfish)	Keenleyside 1972; Dupuis & Keenleyside 1988
Lepomis punctatus (Spotted Sunfish)	DeWoody et al. 2000c
Percidae (Perches)	
Etheostoma flabellare (Fantail Darter)	Knapp & Sargent 1989
Etheostoma kennicotti (Stripetail Darter)	Page 1974
Etheostoma olmstedi (Tessellated Darter)	Constanz 1979, 1985; DeWoody et al. 2000a; Farmer & Alonzo 2008
Etheostoma squamiceps (Spottail Darter)	Page 1974; Bandoli 1997, 2002, 2006
Etheostoma virgatum (Striped Darter)	Porter et al. 2002

1992; Lindström & Sargent 1997). This hypothesis also applies to why males might steal eggs (McKaye & McKaye 1977). Second, a female might use the presence of eggs in a male's nest as a marker that another female has already chosen him (the mate choice effect, Ridley 1978; DeMartini 1987; Goldschmidt et al. 1993; Lindström & Kangas 1996). Accepting another's choice may benefit a female if choice is a faulty process, or by saving her time and energy as well as reducing the predation risk associated with searching for an acceptable mate (Losey et al. 1986; Gibson & Höglund 1992; Dugatkin & Höglund 1995; Kraak 1996). Third, the female is not assessing the eggs at all but is responding to the male's behavior, which has altered subtly to reflect the fact that he was already successful (the elevated courtship effect, Jamieson & Colgan 1989; Jamieson 1994). For example, Threespine Sticklebacks increase their courtship intensity after they acquire their first clutch (van Iersel 1953; Sevenster-Bol 1962; Segaar et al. 1983; Hart 1985; Segaar & de Bruin 1985; Jamieson & Colgan 1989), and male Pecos Pupfish boost their color signal (Kodric-Brown 1996). Fourth, a female improves her clutch's chance of survival because a male who has many clutches has so much to gain, particularly if the spawning season is brief, that he will invest more time in nest guarding and egg cleaning (increased parental care effect, Pressley 1981; Coleman et al. 1985; Sargent 1988; Coleman & Fischer 1991; Sargent & Gross 1993). Many parental fishes do seem to take more risks than their nonparental brethren. For example, male Dollar Sunfish (*Lepomis marginatus*) return to their nests more quickly after the threat of an aerial predator has passed when they have eggs versus no eggs (Winkelman 1996). Other male fishes show an increase in aggression when guarding offspring (i.e., Threespine Stickleback, Huntingford 1976; Pressley 1981; Pumpkinseed, Colgan & Gross 1977; Smallmouth Bass, Ridgway 1988, 1989; Spottail Darters, *Etheostoma squamiceps*, Bandoli 2002). The increase in aggression may translate into allowing predators to approach more closely before the guardian male freezes or flees, responding more intensely to the presence of an intruder, or both. However, whether this increase in risk taking is influenced by the actual size of the clutch, rather than just its presence, is unclear.

The effect of parental effort on clutch survival is also ambiguous. Removal of the father completely leads to widespread clutch destruction, but the relationship between intensity of care and clutch survival is difficult to disentangle from male body size and the effects of clutch size on hatching percentage (Perrin 1995; Bandoli 2002). Presumably some optimal size for total clutch mass exists above which eggs in the center of the clutch will suffer less efficient gas and waste exchange (Perrin 1995). This problem may be exacerbated by the size of the guarding male. For example, small, and to a lesser extent, medium-sized Rock Bass (*Ambloplites rupestris*) hatched fewer fry if they were guarding medium to large brood sizes, so the presence of eggs is not an independent marker of male parental ability (Sabat 1994a). In all, the evidence for females gaining increased paternal investment and thus increased probability of offspring survival by spawning with egg-holding males is suggestive but tenuous at the moment.

Overall, the importance of these four factors likely will vary among clades (reviewed by Jamieson 1995; Suk & Choe 2002). This leads us to the next problem: given the existence of the preference, why would any female be the first to deposit her eggs in a male's nest? For example, most male Pumpkinseeds in a lake containing a high percentage of egg predators (Golden Shiner, *Notemigonus crysoleucas*, and Brown Bullhead, *Ameiurus nebulosus*) eventually abandoned their nests (Popiel et al. 1996); possibly because too few eggs and fry remained to maintain the physiological and neurological threshold required to trigger parental behavior. This physiological response might influence males with only one clutch, driving them to abandon those eggs and try their luck elsewhere (e.g., build another nest or take over another nest). The female who was unlucky enough to be first loses her entire investment in this situation. One solution to the problem might be that abandoned nests are often taken over by other males (Johnston 2000a). For example, becoming a foster father is one way small darter males can solve the dual problems of how to get a territory that includes a large, flat nest rock (which females prefer, Page & Schemske 1978; Constanz 1985) when you are surrounded by larger, more competitive males and, even if you do get a territory, how to attract that first female when mating success is strongly size dependent (e.g., Bandoli 1997). Two of four Striped Darter foster fathers actually succeeded in attracting a mate (the other two had just adopted their nests when the study concluded), so there are apparently benefits to adopting another male's offspring (Porter et al. 2002). If these small males were successful at raising a few clutches, then the female who spawned first with the eventual nest deserter will not suffer as high a penalty in terms of total loss of her investment; the penalty will be conditional on the parental success of the foster father. Darters aside, the question of the benefits to being the first female remains largely unanswered.

Egg Mimics

Breeding males in many species of egg-clustering darters develop white or yellow protrusions on their fins that appear to resemble eggs (egg mimics or spots, Fig. 2.13). These occur on the first dorsal fin in one species group in the subgenus *Catonotus*, the second dorsal fin in a different species group in *Catonotus*, the pectoral fins of the Striped Darter (Porter et al. 2002), the cheeks of the Corrugated Darter (*Etheostoma basilare*, Page et al. 2003), and the pectoral and pelvic fins in some males in some populations of the subgenus *Boleosoma* (Collette 1965; Lindquist et al. 1981; Page & Swofford 1984; Mayden 1985b; Page & Bart 1989; Bart & Page 1991; Page et al. 1992). Males in some species display these protuberances as closely as possible to the nest stone, which suggests the male is trying to deceive the female into thinking he is already guarding eggs (Page & Swofford 1984). Removal of the dorsal fin knobs on Fantail Darter males provided convincing support for this hypothesis (Knapp & Sargent 1989). When matched against knobbed males, the knobless males gathered far fewer clutches. Similar results were documented subsequently for the Guardian Darter (*Etheostoma oophylax*), the Lollipop Darter (*Etheostoma neopterum*), the Egg-mimic Darter (*Etheostoma pseudovulatum*), and the Spottail Darter (Strange 2001).

The relationship may be even subtler than just the presence or absence of egg spots. The number of egg mimics on the pectoral fin and male spawning success were correlated positively in the Striped Darter (Porter et al. 2002). Benefits of egg mimicry are obvious. As discussed above, females in many species with male-only care prefer to spawn with egg holders. The evolutionary pathway of the novel egg spot trait, however, is a complicated one. Males in all percids develop fleshy protuberances on their anal fins, pelvic fins, and ventrally on some scales. Fleshiness is caused by proliferation and eventual keratinization of the epidermal tissue (Bart & Page 1991), producing rough structures that may help males retain contact with females during courtship and mounting (Collette 1977). Darters in the subgenera *Boleosoma* and *Catonotus* have a derived egg-laying behavior (guarding, egg clusterers), a derived courtship sequence (the male positions himself next to the female, rather than mounting her, Winn 1958;

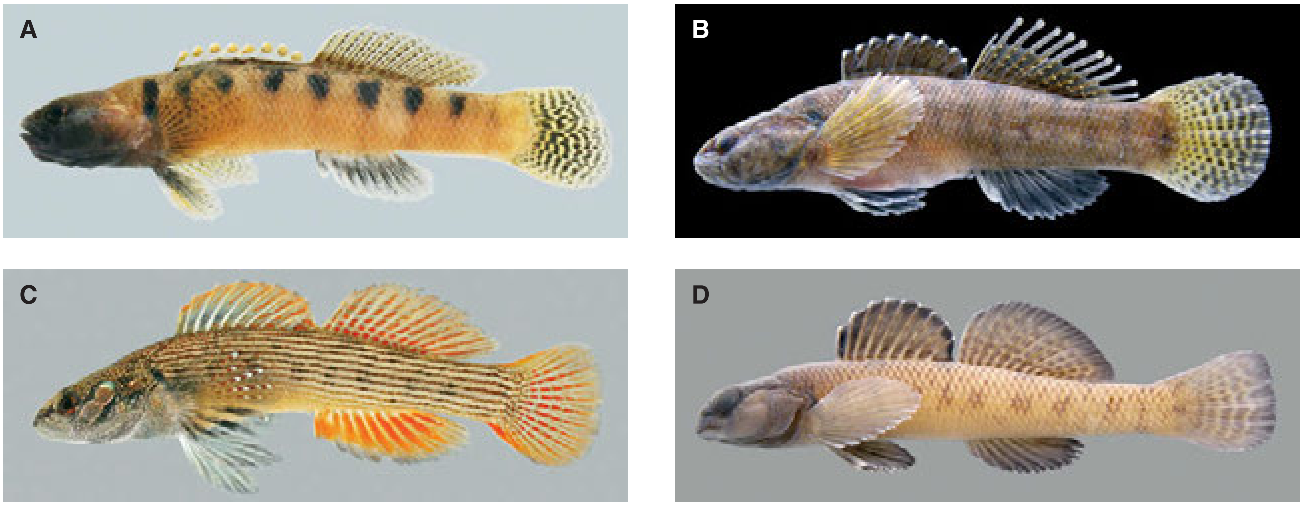

Figure 2.13. Breeding males of some cavity-nesting darters (genus *Etheostoma*) display hypothesized egg mimics to entice breeding females into their nests. Females often select the male that already has eggs in his nest. The hypothesized egg mimics are developed on (*top to bottom*): (A) the first dorsal fin as in the Fantail Darter, *Etheostoma flabellare* (yellowish knobs at the tips of the dorsal fin spines); (B) the second dorsal fin as in the Guardian Darter, *Etheostoma oophylax* (knob-tipped extensions of the soft dorsal fin rays); (C) the pectoral fin and cheek as in the Striped Darter, *Etheostoma virgatum* (white spots on the pectoral fin and egg-like spots on the cheek); (D) the pelvic and pectoral fins as in the Johnny Darter, *Etheostoma nigrum* (swollen whitish tips on the pelvic and pectoral fin rays) (photographs by and used with permission of: Uland Thomas, A, breeding male, small tributary, Kanawah River, Virginia, 21 May 2011; Matt Thomas, B, breeding male, Grindstone Creek, Calloway County, Kentucky, 26 April 2005; Matt Thomas, C, breeding male, Birch Lick Creek, Jackson County, Kentucky, 29 June 2009; Matt Thomas, D, breeding male, Terrapin Creek, Graves County, Kentucky, 6 August 2004).

Page 1985), and derived fleshy protuberances on one of the two dorsal fins or on the paired fins. Members of the subgenus *Catonotus* have an additional apomorphy, fleshy ridges on the scales below the lateral line and behind the pectoral fin insertion point. Mayden (1985b) proposed that these structures have the same function as the ventral protuberances in other groups, stimulation of the female during courtship, the only difference being that the courting pair are now side by side (lateral protrusions) rather than one on top of the other (ventral protrusions).

Lindquist et al. (1981; see also Bart & Page 1991) hypothesized that the fleshy protuberances on the dorsal fins originally functioned to protect eggs on the ceiling of the nest cavity from being damaged by the sharp dorsal fin spines of the guarding male. In some species, the dorsal protuberance was coopted for another function, that of egg mimicry (Page & Bart 1989). Evidently, this new function is associated with increased evolution in the fleshy structures because color is added to either the protuberance itself or the inter-radial membranes around it, which may function to increase its visibility, its egg-like appearance, or both. In the Guardian Darter the egg mimic appears at the beginning of the breeding season and reaches its peak size at the apex of breeding activity. Males have a lateral, fin-flared display when courting females, which would highlight the egg mimic most strongly in the horizontal (length) dimension. Interestingly, the length of the egg mimic was correlated strongly with male body size. This is a fascinating result because it indicates that the morphological trait may be transmitting both deceptive (I have eggs; although this deception disappears after the male acquires his first clutch) and reliable (indicator of body size) information (Page & Knouft 2000). Thus, evolution of egg mimics possibly has involved a variety of selective vectors, protection of eggs from damage by male's fins (benefits both the male and female), reliable indicators of male body size and condition (benefits the female), and unreliable indicators of male parental status (benefits the male).

Nest Associations

Many minnows deposit their eggs over the nests of other fishes, primarily cyprinids or centrarchids (Table 2.4; Figs. 2.14–2.15). Nest association may have arisen originally as a side effect of the tendency displayed by many cyprinid species to rush toward courting conspecifics, eventually forming spawning aggregations. The nest building and courtship displays of host species may also trigger aggregation-forming behavior. Once in the area, associates are then stimulated to spawn by ovarian fluid- and milt-based olfactory cues from the hosts, and this, in turn, attracts more associates (Hunter & Hasler 1965; Shao 1997a). Nest association is thus based on individuals responding to plesiomorphic signals in an inappropriate way. The apparent opportunistic nature of nest association supports its origin as a pleisomorphic side effect. Many associates can spawn in the absence of the host, and some associates are nest builders themselves, serving as hosts in their turn. Most nest-associate systems also appear to be either facultatively or obligatorily mutualistic (Carr 1942; Vives 1988; Wallin 1992; Johnston 1994b). For example, no significant difference occurred in the hatching success of Smallmouth Bass nests with and without Longnose Gar (*Lepisosteus osseus*) eggs (Goff 1984). However, examples exist of the interaction moving to the first stage of an evolutionary arms race. In a variety of systems, both the nest builder and, more usually, the associate were observed eating eggs out of the nest (Table 2.4). Egg eating may have more than just the obvious nutritional benefit if prey species are actually eating the eggs of potential predators (e.g., Dusky Shiner, *Notropis cummingsae*, eating eggs of the Redbreast Sunfish) or competitors.

The inappropriate nature of the nest-association response can only be maintained evolutionarily if the benefits outweigh the costs. The benefits of such behavior to the associate are obvious, including protection from predators for its eggs and fry either via the dilution effect or direct parental care by the nest holder (Johnston 1994a; Shao 1997a), reduction of siltation during the early stages of deposition by the stone-cleaning and -moving behavior of the nest builder (van Duzer 1939), and a great saving in energy that can be directed toward reproduction. The costs to the nest builder also are obvious, including wasted energy caring for and defending offspring of distantly related species and possibly decreased hatching success due to the spread of fungal infections in larger egg masses (Shao 1997b). Assigning benefits to the nest builder is more difficult, although the increase in numbers of eggs in the nest could conceivably reduce predation on its own eggs via the dilution effect (Johnston 1994ab). Host species often ignore the presence of associates (Hunter & Hasler 1965 and references therein), suggesting that the additional cost of rearing other species' offspring is not high enough to justify the time and energy it would take to keep the nest area free of the smaller, faster minnows. Perhaps the decision to attack or ignore is based on the interaction between the density of surrounding

Table 2.4. Nest associates and their host species.

Nest Associate	Nest Holder (host species)	References
Lepisosteidae		
Lepisosteus osseus (Longnose Gar)	Smallmouth Bass (*Micropterus dolomieu*)	Goff 1984
Cyprinidae		
Campostoma anomalum (Central Stoneroller)	Hornyhead Chub (*Nocomis biguttatus*), Bluehead Chub (*Nocomis leptocephalus*), Bigmouth Chub (*Nocomis playtrhynchus*), Bull Chub (*Nocomis raneyi*), River Chub (*Nocomis micropogon*), Creek Chub (*Semotilus atromaculatus*)	1; 3; Raney 1947; Miller 1964; Johnston 1994a; Maurakis 1998
Chrosomus cumberlandensis (Blackside Dace)	Largescale Stoneroller (*Campostoma oligolepis*), Creek Chub	3
Chrosomus erythrogaster (Southern Redbelly Dace)	Hornyhead Chub, Bluehead Chub, Central Stoneroller, River Chub	1; 3; Etnier & Starnes 1993; Cicerello & Landermilk 1996
Chrosomus oreas (Mountain Redbelly Dace)	Bluehead Chub, Bigmouth Chub, Bull Chub	1; 2; Maurakis 1998
Chrosomus saylori (Laurel Dace)	Possibly Largescale Stoneroller	Skelton 2001
Clinostomus elongatus (Redside Dace)	Creek Chub, Zander (*Sander lucioperca*), Common Shiner (*Luxilus cornutus*)	1; 3
Clinostomus funduloides (Rosyside Dace)	Bluehead Chub	Maurakis et al. 1991a; Johnston 1994a
Cyprinella lutrensis (Red Shiner)	*Lepomis* spp.	3
Erimyzon sucetta (Lake Chubsucker)	Florida Bass (*Micropterus floridanus*)	Carr 1942
Hybopsis hypsinotus (Highback Chub)	Bluehead Chub	Johnston 1991
Luxilus albeolus (White Shiner)	Tonguetied Minnow (*Exoglossum laurae*)	Jenkins & Burkhead 1994
Luxilus cerasinus (Crescent Shiner)	Bluehead Chub	1; 3
Luxilus chrysocephalus (Striped Shiner)	Bluehead Chub, Central Stoneroller, Creek Chub, Bigmouth Chub, Bluntnose Minnow (*Pimephales notatus*), Silver Shiner (*Notropis photogenis*), Cutlip Minnow (*Exoglossum maxillingua*)	3; Maurakis et al. 1991ab; Gleason & Berra 1993; Maurakis 1998
Luxilus coccogenis (Warpaint Shiner)	River Chub (*Nocomis micropogon*)	1; 3
Luxilus cornutus (Common Shiner)	Central Stoneroller, River Chub, Creek Chub, Hornyhead Chub, Bull Chub, Tonguetied Minnow, Cutlip Minnow, Bluntnose Minnow, Silver Shiner, Fallfish (*Semotilus corporalis*), Smallmouth Bass (*Micropterus dolomieu*); may contribute to maintenance of nest by picking up pieces of gravel (nest cleaning); associate eats eggs	1; 3; Maurakis et al. 1991ab; Gleason & Berra 1993; Jenkins & Burkhead 1994; Maurakis 1998
Luxilus pilsbryi (Duskystripe Shiner)	Hornyhead Chub, *Campostoma* spp.	3
Luxilus zonatus (Bleeding Shiner)	Hornyhead Chub, *Campostoma* spp.	3
Luxilus zonistius (Bandfin Shiner)	Bluehead Chub, Bluefin Stoneroller (*Campostoma pauciradii*)	3; Walser et al. 2000; Herrington & Pop 2004
Leuciscus rutilus (Roach)	Zander	1
Lythrurus ardens (Rosefin Shiner)	Bigmouth Chub, *Lepomis* spp., Bluehead Chub, Bull Chub	1; 3; Maurakis et al. 1991a; Maurakis 1998
Lythrurus bellus (Pretty Shiner)	*Lepomis* spp.	3

(continued)

Table 2.4, continued

Nest Associate	Nest Holder (host species)	References
Lythrurus umbratilis (Redfin Shiner)	Green Sunfish (*Lepomis cyanellus*), Longear Sunfish (*Lepomis megalotis*)	1; 3; Noltie & Smith 1988; Johnston 1994ab
Nocomis biguttatus (Hornyhead Chub)	Common Shiner; associate eats eggs	2
Notemigonus crysoleucas (Golden Shiner)	Redbreast Sunfish (*Lepomis auritus*), Pumpkinseed (*Lepomis gibbosus*), Bluegill (*Lepomis macrochirus*), Spotted Sunfish (*Lepomis punctatus*), Green Sunfish, Largemouth Bass (*Micropterus salmoides*), Bowfin (*Amia calva*); will only spawn over nests whose builder is attracting conspecific females (study with Pumpkinseed)	3; Shao 1997ab; Katula & Page 1998
Notropis amoenus (Comely Shiner)	*Nocomis* spp.	3
Notropis baileyi (Rough Shiner)	Bluehead Chub, Bluefin Stoneroller	3; Johnston & Kleiner 1994; Walser et al. 2000; Herrington & Pop 2004
Notropis chiliticus (Redlip Shiner)	Bluehead Chub	Johnston 1991
Notropis chlorocephalus (Greenhead Shiner)	Bluehead Chub	Johnston 1991; Johnston 1994a
Notropis chrosomus (Rainbow Shiner)	Bluehead Chub	Johnston & Kleiner 1994
Notropis cummingsae (Dusky Shiner)	Redbreast Sunfish; associate eats host eggs	Fletcher 1993
Notropis leuciodus (Tennessee Shiner)	River Chub	3
Notropis lutipinnis (Yellowfin Shiner)	Bluehead Chub	3; Wallin 1989, 1992
Notropis maculatus (Taillight Shiner)	Florida Bass (*Micropterus floridanus*)	3
Notropis nubilus (Ozark Minnow)	Hornyhead Chub	3
Notropis procne (Swallowtail Shiner)	*Lepomis* spp.	3
Notropis rubellus (Rosyface Shiner)	Hornyhead Chub, Bigmouth Chub, Bull Chub, River Chub, Creek Chub, Common Shiner, Fallfish, Cutlip Minnow; associate eats eggs	2; 3; Maurakis et al. 1991ab; Maurakis 1998
Notropis rubricroceus (Saffron Shiner)	River Chub	1
Notropis semperasper (Roughhead Shiner)	Cutlip Minnow; over nest, but spawning not observed	Maurakis et al. 1991b
Notropis topeka (Topeka Shiner)	Green Sunfish, Orangespotted Sunfish (*Lepomis humilis*)	Pflieger 1997
Phenacobius crassilabrum (Fatlips Minnow)	*Nocomis* spp.	3
Pteronotropis hubbsi (Bluehead Shiner)	Warmouth (*Lepomis gulosus*)	Fletcher & Burr 1992
Pteronotropis welaka (Bluenose Shiner)	Longear Sunfish; observed eating host eggs	Johnston & Knight 1999
Rhinichthys cataractae (Longnose Dace)	River Chub	Raney 1940; Cooper 1980
Semotilus atromaculatus (Creek Chub)	Central Stoneroller	1
Percidae		
Etheostoma spectabile (Orangethroat Darter)	Smallmouth Bass	Pflieger 1966

1=references in Hunter & Halser 1965; 2=references in Fletcher 1993; 3=references in Johnston & Page 1992.

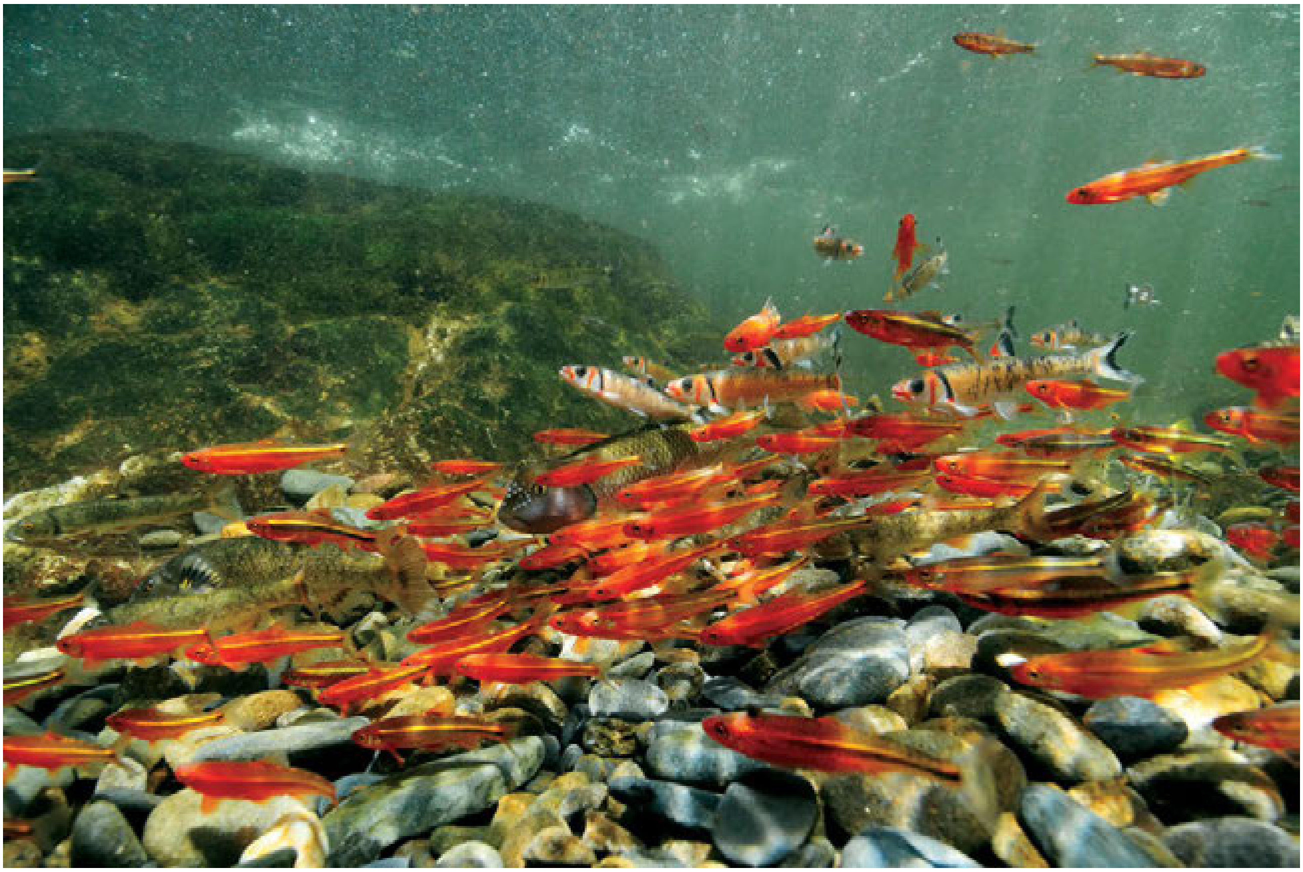

Figure 2.14. Nest associates spawn over the nests of other fish species and are especially common among North American minnows (Carps and Minnows, Cyprinidae). A swarm of nest associates, all cyprinids, jockey to spawn over the gravel mound nest of a River Chub, *Nocomis micropogon*, another cyprinid (large fish with dark head left of center). Associates are the Warpaint Shiner, *Luxilus coccogenis*, Tennessee Shiner, *Notropis leuciodus*, Saffron Shiner, *Notropis rubricroceus*, and Largescale Stoneroller, *Campostoma oligolepis* (Pigeon River drainage, Sevier County, Tennessee, 30 May 2011; photograph by and used with permission of Lance Merry).

associates, the density of conspecific intruders, and the stage a host male has reached in his breeding cycle. There has been little investigation of the mechanisms involved in making that decision.

Oddly, some minnows spawn over the nests of large piscivores such as basses (*Micropterus* spp.) and the Bowfin (*Amia calva*). Associates should benefit from the extended period of parental care shown by these piscivorous species, and indeed, field observations support this suggestion. Nesting male Largemouth Bass (*Micropterus salmoides*) guard mixed-fry groups comprising their own offspring and Golden Shiner (*Notemigonus crysoleucas*) fry (Kramer & Smith 1960), Florida Bass (*Micropterus floridanus*) guard their own and Lake Chubsucker (*Erimyzon sucetta*) fry (Carr 1942), and Smallmouth Bass protect their own and Common Shiner (*Luxilus cornutus*) fry. So, why does the predatory nest holder not eat the associates? The most obvious explanation for this apparent truce between predator and prey is that feeding behavior is suppressed in parental males, and the nest associate takes advantage of this brief respite. This is yet another aspect of North American freshwater fish behavior that requires further research.

THE IMPORTANCE OF SPERM: ALTERNATIVE MALE MATING STRATEGIES

Evolutionarily, the mandate is to reproduce as often as you can with the highest-quality mate you can find, then die. Before the early 1980s, many biologists would have said that large, dominant males controlled most mating systems (e.g., Simanek 1978). Small males rarely got to

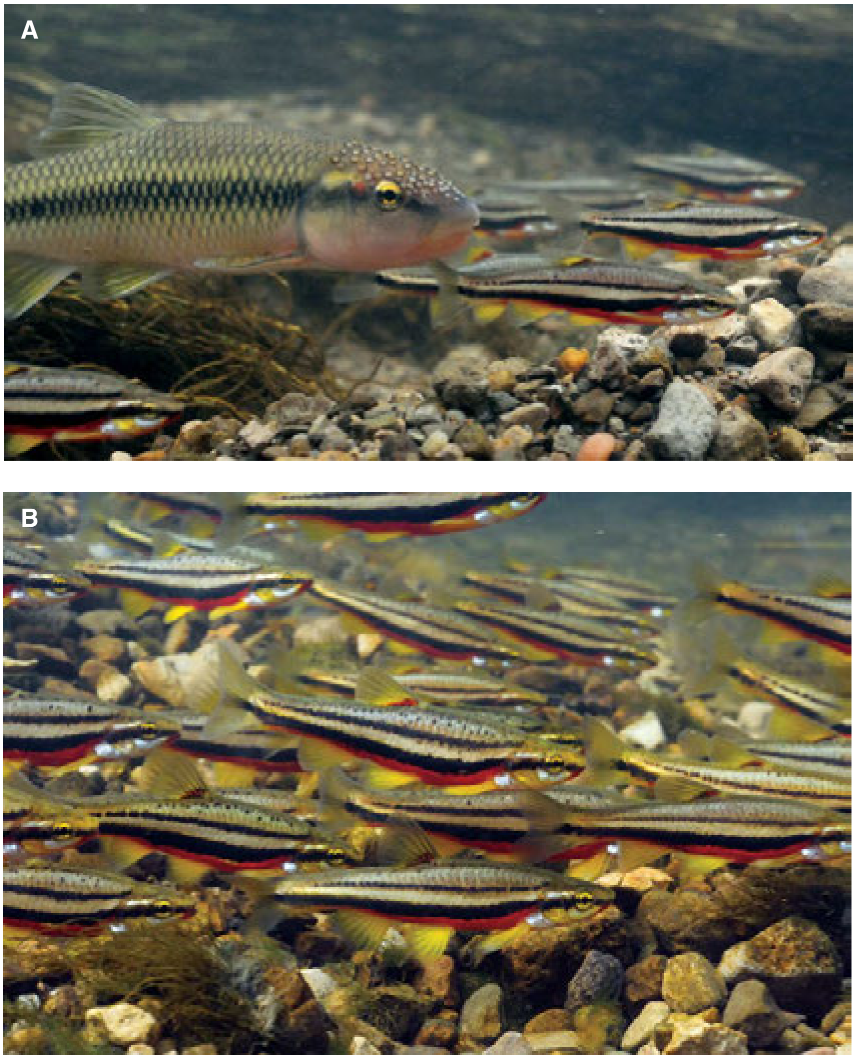

Figure 2.15. Southern Redbelly Dace, *Chrosomus erythrogaster*, gather to spawn over the active gravel mound nest of a male Hornyhead Chub, *Nocomis bigutattus* (*top*). The nest builder, the Hornyhead Chub, is the large fish to the left. Close-up of some of the hundreds of Southern Redbelly Dace (*bottom*) that aggregated to spawn over the nest (tributary, Mackinaw River, Woodford County, Illinois, 20 May 2012; photographs by and used with permission of Lance Merry).

see Paris before they died. Over the past 30 years, however, this perception was modified as evidence mounted showing that mating systems are often far more complicated than previously thought. For example, the type of breeding system used by male Pecos Pupfishes depends on the size of the available breeding habitat and the density of the Pupfish population. Males are territorial if living in a large area regardless of density or if living in a small area under high densities but form a dominance hierarchy if living in a small area under low densities (Kodric-Brown 1988).

The full extent of mating system complexity was revealed by the discovery of alternate male mating tactics (reviewed in Waltz 1982; Austad 1984; Dominey 1984). Some fishes have a social system in which larger males defend spawning sites and/or females and smaller (kleptogamic) males act as either satellites (female mimics) or sneakers. Depending on the species, kleptogamic males attempt to either rush in at the critical moment of gamete release and add their own genetic complement to the swirling mixture of eggs and sperm or force copulations on females. If the two tactics, large courting versus small kleptogamic, are genetically determined, lifetime fitness should be equivalent between the behavioral types (Maynard Smith 1982). If the tactics are condition dependent (Parker et al. 1996; Parker 1998) with males adopting a particular behavioral role depending on their size, the fitness of the different tactics need not be equivalent (Repka & Gross 1995) and may fluctuate as environmental and social parameters change in a population (reviewed by Taborsky 1994; Gross 1996; Thomaz et al. 1997). For example, Bluehead Shiner (*Pteronotropis hubbsi*; but see Mayden et al. 2006) males exist in two distinct subclasses: small, bluer-headed, secondary males and large-bodied, large-finned terminal males. Secondary males have relatively larger testes for their body size, which suggests that they may function as sneakers. On the other hand, secondary males eventually become terminal males, so the males apparently are playing a double strategy: increased rate of gonadal growth in early stages of development (when small be a sneaker) followed by an increase in the relative rate of somatic growth (when large be terminal) (Fletcher & Burr 1992). The Bluehead Shiner is sister to the Bluenose Shiner (*Pteronotropis welaka*) plus the Redeye Chub (*Notropis harperi*) (Amemiya & Gold; Simons et al. 2000, 2003; Mayden et al. 2006). Neither of the latter species have two distinct male morphs; gonadal and somatic growth increase with age. If these two breeding systems remain distinct on further experimental scrutiny, this would be an ideal group in which to study the behavioral, ecological, and life history parameters underlying the evolution of alternate male reproductive strategies (Johnston & Knight 1999).

The mechanism underlying the developmental decision to become a large or small male is not well understood but must ultimately depend on a complicated interaction between the individuals' genotype and life history parameters such as egg size, amount and composition of yolk, and vagaries of the environment. The most important of these vagaries are the effects of food supply and nutrition, habitat availability, predation pressure, and social conditions on growth rate (swordtails, Borowsky 1973, 1978; Fathead Minnows, Danylchuk & Tonn 2001; Salmonidae, Trouts and Salmon, Gross 1991b; Piché et al. 2008 and references therein; Bluegill, Aday et al. 2003) since body size influences social status and reproduction in so many fishes (Huntingford & Turner 1987; Ridgway et al. 1991; Danylchuk & Fox 1996).

Alternative Mating Strategies in Sunfishes

Sunfish in the genus *Lepomis* all have the same basic breeding system (Breder 1936; descriptions of behaviors by Miller 1963; Warren 2009). Males establish territories and build shallow nest depressions by sweeping gravel and debris away with their caudal fins. Females visit several territorial males, then spawn and desert the nest, leaving all of the parental care from eggs through fry to the male (cf. monogamy in other centrarchids, Largemouth Bass, DeWoody et al. 2000b; Smallmouth Bass, Wiegmann et al. 1992; Wiegmann & Baylis 1995). Large males are territorial; small males (when present) adopt either a satellite or sneaker tactic (Keenleyside 1972; Dominey 1980; Gross 1982); the small male tactic may be age dependent (Ehlinger et al. 1997). Some species of Sunfish have both kleptogamic male types (e.g., Bluegill), but other species appear to have only one type (e.g., only sneakers in the Redbreast Sunfish and Pumpkinseed). During courtship, both partners circle the nest with the male on the outside. When ready to deposit eggs the female tilts at almost a 90 degree angle to the male, bringing her vent close to his, facilitating simultaneous release of gametes (Keenleyside 1972). Both the circling and female tilting behaviors attract the attention of neighboring conspecifics, particularly the vigilant kleptogamic males.

Reproductive success of the alternate tactics is dependent on a delicate, negative frequency-dependent (Gross 1984, 1991a, 1996; but see Ryan et al. 1992) balance between the advantages of being small (early maturation, longer reproductive cycle) versus the advantages of being large (female preference, winners in agonistic encounters) (Jones 1959; Noltie & Keenleyside 1986; Sandercock 1991; Gage et al. 1995). These benefits must, of course, be weighed against the costs. For example, consider two problems attached to being a small male. Small individuals may have a higher overwinter energy deficit than large individuals, which may delay gonadal maturation, the initiation of spawning, and the length of spawning activity the following spring (Ridgway et al. 1991; Danylchuk & Fox 1996). Costs are also dependent on the intensity of predation in the population and, more importantly, whether that predation is size-specific. If predators selectively attack small males, then the advantages of being a sneaker are decreased by the costs of being eaten (Gross 1991a). If possible (e.g., the tactic used by an individual male is flexible), males living in an area with a high predator density should allocate more energy to growth, delaying reproduction until they are too large to be attacked (Reznick & Endler 1982; Crowl & Covich 1990). This is exactly what happens to Bluegills in reservoirs with different predator communities. Males in a reservoir with high densities of Largemouth Bass (selectively prey on juveniles) were older and larger at maturity (fewer sneakers) than males in areas with few bass but many fishers (selective predation on larger fish) (Belk & Hales 1993).

Mathematical models predict that large and small males will have equivalent fitness at an equilibrium point between the densities of both male types in the population. Because the equilibrium point is dependent on the interaction of two factors (probability of survival to maturity and breeding success), it is expected to vary from population to population, and possibly across species as well (Gross 1991ab). A microsatellite DNA analysis of paternity in one population of Bluegills indicated that paternal males fertilized an average of 76.9% of the eggs they were guarding, leaving the remaining 23.1% to be subdivided among satellite and sneaker males (Neff 2001). When these data were combined with estimates of paternity from four other colonies (100, 85.6, 73.5, and 41.3%, Philipp & Gross 1994) an interesting result emerged. Since only 22% of males are kleptogamic within Bluegills as a whole (Gross & Charnov 1980; Gross 1982), the distribution of fertilizations is consistent with the proportion of territorial and kleptogamic males. This result indicates that fitness is about equal for one component of fitness (fertilization success) across the two tactics in Bluegills.

Fertilization success, in turn, is the outcome of the following interactions between parental and cuckolder sperm (Neff et al. 2003). Sneaker sperm are activated faster because they have more ATP (Burness et al. 2004). Given that the majority of eggs are fertilized within 5–10 s of ejaculation, this ability might favor sneakers, although fertilization also will be influenced by the position of each male relative to the female when she spawns. Parental sperm live longer, possibly allowing fertilization to occur should a female release eggs over the nest already containing eggs while the male is engaged elsewhere. Cuckolders produce more concentrated ejaculate, but the volume is so much smaller than that of a large male that the sneaker ejaculate contains about 400 million fewer sperm/ejaculate (Leach & Montgomerie 2000). Additionally, once activated the sperm from older nest holders swam faster than the sperm of their younger competitors and sneakers (sneaker sperm was about 73% slower, Leach & Montgomerie 2000; Casselman & Montgomerie 2004).

Clearly, the relationship among sperm volume, sperm quality, spawning behavior, and fertilization success is a complex one. There is, moreover, more to lifetime fitness than just fertilization success. For example, parental Bluegill males who were cuckolded fanned their nests at a lower rate (Neff & Gross 2001), defended the nest less vigorously (see also Pumpkinseed, Rios-Cardenas & Webster 2005), and were more likely to either abandon or eat part of their brood (Neff 2003ab). Males can use fry-based olfactory cues to identify their own offspring (Neff & Sherman 2003), so they may be selectively cannibalizing the cuckolders' offspring. The fitness pendulum swings in favor of paternal males. But cuckolders take heart. A number of factors move the pendulum back toward sneakers. Females may release ≥3 times as many eggs when spawning with a territorial male if a cuckolder is also present (Fu et al. 2001). Once the eggs are fertilized, sneaker offspring grow faster during the first 8 days of development (see also Atlantic Salmon, Grant et al. 2002a) and suffer fewer successful attacks by the Alberta Hydra (*Hydra canadensis*) than their smaller relatives (Neff 2004). The pendulum swings toward the sneaker, but does it strike the required balance? Data are still required for other fitness components, including estimates of survivorship, in order to answer this question (Ryan et al. 1992).

Cuckolding males are not always small sneakers in Sunfishes. In an extensive study of mating success in the Longear Sunfish, *Lepomis megalotis*, Jennings and Philipp (1992) recorded 640 cuckoldry events. Of those, 586 came from neighboring territorial males and 16 were from non-nesting large males, leaving only 38 (6%) from small sneakers (see also about 2% in Spotted Sunfish, *Lepomis punctatus*, DeWoody et al. 2000c; <5% in Redbreast Sunfish, DeWoody et al. 1998; no kleptogamic males in Dollar Sunfish, MacKiewicz et al. 2002). Central Longear Sunfish nest in colonies with some peripheral males holding solitary nest sites. Models for the evolution of colonial nesting generally focus on the power of females to shape male advertisement displays. Female-initiated models predict that females prefer to spawn in a colony because of the increased protection against brood predation (Dominey 1981; Gross & McMillan 1981), the increased opportunity to assess potential mates, or both (Alexander 1975; Bradbury 1981). If either of these factors is at play in the system, then dominant males should nest in colonies, leaving subordinates to fend for themselves on the periphery, females should discriminate against solitary males, and larger colonies should have better overall reproductive success / male than smaller ones.

None of these predictions were corroborated for the Longear Sunfish. Females did not discriminate against solitary males, solitary males were larger than colonial nesters, and no differences occurred in intermale mating success depending on colony size (Jennings & Philipp 1992). The same result was reported for Northern Longear Sunfish, *Lepomis peltastes*, populations (Dupuis & Keenleyside 1988) and for Bluegills (Neff et al. 2004). The distribution of males, cuckolding, and female matings indicated that colony formation was being driven by two interacting forces: female preference for larger males and the counterstrategy by less-preferred males of clustering around a larger rival to increase opportunities for cuckoldry (Bietz 1981; Beehler & Foster 1988). Large males have a choice of nest strategy: be solitary and avoid sneakers (no solitary males were cuckolded) but expend energy defending against territory establishment by other males; or accept the presence of neighbors, save energy, but pay the price in an increased risk of cuckoldry. As in the Bluegill system, the ebb and flow of colonial versus solitary nesters will depend on the size distribution of males in the population.

Yet another variable needs to be taken into account. Unlike their Bluegill relatives, Longear Sunfish males will only court and spawn with one female at a time and stop courting altogether 2 days after fertilizing their brood. Females who approach courting or guarding males are rejected and often turn to less preferred nest holders as a consolation prize. Presumably ready access to another, albeit less preferred, mate saves females the time, energy, and risk incurred in searching for and courting another mate. This change in male reproductive biology gives added impetus to forming clustered nests since less preferred males can hope to spawn with disappointed females simply by being in the right place at the right time (Beehler & Foster 1988). Overall, the Longear Sunfish breeding system is quite different from that reported for Bluegill, indicating that the degree of cuckolding by large and small males, the focus of female choice, and the details of male parental physiology with its subsequent effects on sexual behavior probably will interact in unique ways among species of *Lepomis*, perhaps even among populations of the same species.

Alternative Mating Strategies in Salmonids

Salmonid species usually contain two or three male morphs; large, late-maturing sexually dimorphic (e.g., snout length, hump size), dominant males (the "smilies" or "tyee" of Canadian West Coast fishers) and early-maturing medium-sized jacks, small parr, or both. The mating tactics used by these males range from compete for access to females, sneak occasionally (large males) through compete for access to females, or sneak according to social condition (jacks) to always sneak (parr). Males tend to migrate upstream and arrive on the spawning grounds first, where large males and some jacks, when present, begin competing vigorously for social status (Järvi 1990; Fleming et al. 1996; Quinn et al. 1996). Females arrive and begin competing for access to nesting sites. Larger and heavier females have an advantage in this competition (Fleming et al. 1997) and tend to choose sites in the better-oxygenated, shallow waters near shore (Sockeye, Foote 1990; Quinn & Foote 1994; Coho Salmon, van den Berghe & Gross 1986).

A female digs the nest by tilting to one side and sweeping the gravel substrate with her caudal fin (redd construction), probing the substrate occasionally with her anal fin. As she approaches ovulation and egg deposition, the intensity of digging decreases, while probing increases and stabilizes (Atlantic Salmon, de Gaudemar & Beall 1999 and references therein). Males respond to these subtle cues, choosing to court females closest to egg deposition (Chum Salmon, *Oncorhynchus keta*, Schroder 1981). A male responds to the initial digging and probing by swimming around the female, then, as digging frequency begins to decrease, swimming across her caudal peduncle or back. During each episode of probing, he lines up beside the female, quivering along her flank from her anal fin to her operculum. Reacting to the subtle cue (stabilization of probing) the male then begins to quiver toward the female's head, thus aligning the partners in the optimal position for simultaneous release of sperm and eggs. In at least one salmonid species (landlocked Sockeye Salmon), this synchronization involves an interaction between visual and vibrational cues. Low-frequency vibrations (2 Hz) caused by female digging and early probing increase levels of plasma 17,20β,-dihydroxy-4-pregnen-3-one and expressible milt in males (Moore & Waring 1999), as well as provoking courtship quivering. When the female increases her rate of probing, the vibrational frequency also increases (5–21 Hz), releasing male alignment and ejaculation (Satou et al. 1994a). This interaction highlights yet another poorly studied sensory modality involved with courtship communication in North American freshwater fishes, the near-field lateral-line system (Satou et al. 1994b).

During this period of gamete release males are most vulnerable to sneakers. Although large males dominate small males for access to females, they can rarely restrict all access (Esteve 2005 and references therein; Jacob et al 2007). Large females in particular attract many males, creating a defensive nightmare for their mate (Quinn et al. 1996) and increasing the chances for sneak spawnings. Because fertilization is extremely rapid following gamete release (5–10 s), successful fertilization may be influenced more strongly by male position and the timing of egg and sperm release than by any characteristics of the sperm themselves (Hoysak & Liley 2001; Liley et al. 2002). It thus becomes imperative from a guarding male's perspective to release sperm as close as possible to the eggs to thwart sneaking attempts (Keenleyside & Dupuis 1988; Fleming 1996) and increase fertilization efficiency (Schroder 1982; Chebanov et al. 1983; Gross 1984, 1985; Maekawa & Onozato 1986; Hutchings & Myers 1988; Mjølnerød et al. 1998). For example, a Rainbow Trout male moves his gonopore to <30 mm from his partner's gonopore and begins to ejaculate slightly before she releases her eggs (FitzPatrick & Liley 2008). The need to align so closely may, in turn, have modified mate choice in salmonids. Unlike males in many other fishes, courting males do not make mating decisions based on absolute female size. Instead of "pick the biggest female," the rule used by salmonid males appears to be a relative one of "choose the receptive female closest to your own size" (*Oncorhynchus nerka*, Hanson & Smith 1967; Foote 1988; Foote & Larkin 1988; *O. keta*, Schroder 1981).

The relationship between reproductive success and body size is a fluid one for medium to large males. Jacks and larger, older Sockeye Salmon males had about equal spawning success (Foote et al. 1997) with larger males also occasionally enjoying the benefits as sole guarding partners (Fleming 1996; see Magnhagen 1994 for similar result with Common Gobies). For large- and medium-sized males, reproductive success is affected by the density of competitors, the male's time of arrival on the breeding ground, his condition at that time (reproduction for both sexes is extremely energetically costly, especially for semelparous species, Healey et al. 2003), the distribution and number of receptive females (Dickerson et al. 2004; Seamons et al. 2004ab), and female condition. For example, synchronization between partners in Atlantic Salmon increased for the first three ovipositions, then began to disintegrate over the next three. Hypothetically the female may become less attractive to her mate after the first three bouts because the number of eggs deposited / breeding bout begins to decrease as the female gets more exhausted and depletes her store of eggs (Fleming 1996; de Gaudemar & Beall 1999; de Gaudemar et al. 2000). At this time males may abandon their mates (Crisp & Carling 1989), searching for females at an earlier stage in their cycle. Additionally, the cost of mate guarding is not trivial and may change the dynamics of the system as dominant males begin to drop out of the competitive pool (Morbey 2003), creating in effect, a cascading and relative, rather than an absolute, dominance hierarchy. All these variables combine to produce an extremely dynamic system, as males move between digging females, pause to spawn, then move again (Quinn et al. 1996).

The relationship between size and reproductive success is superficially less fluid when comparing large versus parr males. Sneaker males have a larger GSI (gonad somatic index) and, in some cases, more motile sperm that survive longer when compared with the sperm of large males (Daye & Glebe 1984; Gage et al. 1995; Fleming 1996; Vladic & Järvi 2001). This disparity in GSI, however, may not always translate into an absolute advantage in sperm production because, as noted for Bluegills, large males have absolutely larger testes (Kazakov 1981; Gjerde 1984). In one population of Atlantic Salmon, the average ejaculate size of migrant, courting males is 20–30 times larger than that from the stay at home parr. And, as noted before, position may have primacy over sperm characteristics anyway. Overall, although parr males are quite successful in populations with few migrant males (Atlantic Salmon, Thomaz et al., 1997), large males almost always have the advantage in terms of the percentage of eggs fertilized (Hutchings & Myers 1988; Jordan & Youngson, 1992; Fleming & Gross 1994; Quinn & Foote 1994; Thomaz et al., 1997; Thompson et al. 1998; Blanchfield & Ridgway 1999). As discussed in the Sunfish example, fitness equivalence is determined by calculating the success of an individual tactic relative to the representation of males showing that tactic across populations. Once again, as in the Sunfish system, only one aspect of the model is confirmed. Large males have higher breeding success than sneakers in one reproductive season. In order to determine whether the tactics do demonstrate equal fitness, however, fertility and survivorship data need to be collected from as many populations within each species as possible.

Finally, reproductive success may vary within the sneaker class itself if larger sneakers are usually more successful than smaller ones, presumably because male size determines position in the inter-sneaker dominance hierarchy and this, in turn, affects placement beside the spawning female (Miyabe Charr, *Salvelinus malma miyabei*, Maekawa 1983; Atlantic Salmon, Jones & King 1952; Myers & Hutchings 1987; Hutchings & Myers 1988; Huntingford et al. 1990; Thomaz et al. 1997; Thompson et al. 1998; Masou Salmon, *Onchorhynchus masou*, Koseki & Maekawa 2000). For their part, females dislike sneaker males, and will often attack them and avoid spawning (Maekawa & Hino 1986), so there appear to be some advantages to being small (get closer to females during the scrum around her, Coho Salmon, Gross 1985; better able to hide and be cryptic, Fleming 1998). Thus, opposing selection vectors likely act on sneaker body size, the outcome of which will fluctuate with variables such as the density of sneaker males, availability of refuges, and operational sex ratio.

The existence of alternative reproductive tactics in salmonids has profound implications for management strategies. Gross (1991b) predicted that the evolutionary response to over-harvesting large anadromous males would not be toward replacing those increasingly rare males in the population, but rather toward increasing the proportion of jack males. In other words, the system is not going to compensate for our selective removal of one male type. It is simply going to establish a new equilibrium point at which all males have lower fitness, which in turn, may have negative implications for population persistence. This scenario was further exacerbated if debris from logging accumulated in the spawning streams, or if water level was lowered due to irrigation or to hydroelectric or flood control projects, because both factors increased the refuge available for small males (for details, see Gross 1991b).

One final twist is worth mentioning before I move to another clade. Strong competition for access to breeding females may have more benefits than just the choice of a superior mate. Garant et al. (2001) collected microsatellite DNA data from 650 fry, 41 male, and 35 female spawning Atlantic Salmon. They discovered that, contrary to current assumptions about the relationship between female size, fecundity, and reproductive success, the number of mates a female had had was a far better predictor of offspring number than was body size (a similar result was reported for Coho Salmon, Holtby & Healey 1986). Polyandry carries many potential benefits, including hedging your bets in an unpredictable environment by producing genetically diverse offspring (Petrie & Kempenaers 1998), reducing potential costs of inbreeding (Stockley et al. 1993), and reducing the deleterious effects of genetic incompatibility between partners (Tregenza & Wedell 1998). Garant et al. (2001) cautioned that their results might be an artifact of offspring sampling, but the results are intriguing nonetheless and should be investigated for other salmonid species that also inhabit highly variable environments.

Alternative Mating Strategies in Livebearers

A variety of poeciliid species exhibit a genetic polymorphism for male body size that is correlated strongly with the development of secondary sexual characters (e.g., extensions of caudal fin rays to form a sword in some species of *Xiphophorus*, enlarged dorsal fins and bright colors in some species of *Poecilia*) and behavior (courting versus sneaking, Sailfin Molly, Farr et al. 1986; Travis & Woodward 1989; Travis 1994; Perugia's Limia, Erbelding-Denk et al. 1994; Panuco Swordtail and Barred Swordtail, Ryan & Causey 1989; Zimmerer & Kallman 1989; Morris & Ryan 1990). Variation in male body size is determined by size at maturity (Travis et al. 1989), and this, in turn, is controlled by variation in the Y-linked pituitary (P) locus (Panuco Swordtail and Barred Swordtail, Kallman, 1984, 1989). All males adjust their sperm output based on the availability of a female and her size (more sperm when presented with a larger female). Although small males increase that output dramatically, large males still produce more sperm absolutely (Aspbury & Gabor 2004). Small males reach sexual maturity earlier than their large brethren and have a longer breeding life. Females, however, prefer larger, courting males (Ryan et al. 1990; Schlupp et al. 1994; Marler & Ryan 1997; Witte & Ryan 1998) and may actively associate with them or actually increase their cooperation during mating attempts (Ptacek & Travis 1997). This choice is tempered by male-male interactions; both within and among male types, larger males actively chase intermediate and smaller males away from females in the field and block access to the female in the lab. Large males thus compensate for their slow temporal start by controlling access to females (Baird 1968; Parzefall 1973, 1979; Morris et al. 1992). The intersection of both female-male and male-male interactions thus favors large, courting males. Since male size at maturity has a genetic basis (narrow sense, allelic-based, heritability for body size in the Panuco Swordtail is 91%, Ryan & Wagner 1987; Kallman 1989), we might expect selective pressures based on female preferences and male-male competition to gradually decrease the proportion of small males in the population. Oddly, the frequency of small and large males is relatively stable across seasons in some populations (Snelson 1976; Farr et al. 1986), so how are small males being maintained?

The answer appears to be one that applies generally across many species with alternative male mating tactics. Females attract and court several large males, which spend time trying to block each other's access to the female, allowing sneakers the chance to dart in. A small male capitalizes on these opportunities by swimming up from behind and slightly below the female, swinging his gonopodium forward and attempting to copulate with her (Sumner et al. 1994; Travis 1994). Small males use a forced copulation strategy successfully in the laboratory (Farr et al. 1986), attempting more gonopodial thrusts over a longer reproductive lifetime than their larger rivals (poeciliid sneakers may attempt to mate ≤1/min, Peden 1972; Martin 1975; Magurran & Seghers 1994; Bisazza & Marin 1995; Godin 1995). In fact, the inverse relationship between body size and gonopodial thrusting rate may be plesiomorphic within the poeciliids (Bisazza & Pilastro 1997). Although these attempts generally are directed toward females across all stages of their fertility cycle, female poeciliids are capable of storing sperm for several months (van Oordt 1928; Winge 1937; Vallowe 1953; Baerends et al. 1955). Sperm viability, however, decreases with storage time (van Oordt 1928; Vallowe 1953; Hildemann & Wagner 1954), so the last male to inseminate a female before she ovulates has a fertilization advantage (Rosenthal 1952; Constanz 1984). If most females mate with large, courting males at the peak of their cycle, then sperm from the sneakers is at a disadvantage. The extent of that disadvantage will depend on the percentage of females who experience a forced copulation close to their peak fertility.

As discussed previously, large Sailfin Molly males (Fig. 2.2) are better at detecting the peak fertility stage than are small males; they are not as interested in gravid (pregnant) females (Ptacek & Travis 1997). Male interest is apparently first based on visual stimuli associated with female body shape. Gravid females have a rounder, extended abdomen than postpartum ones. Once potential mates are identified visually, all males move to the next stage of assessment, nibbling around the female's gonopodial area, sampling the estrogen-based olfactory cues (Farr & Travis 1986). Female Sailfin Mollies do not cycle together (Farr & Travis 1989), so on any given day, only a small number of receptive females are available. These females are surrounded by a whirl of large, courting males (which responded more quickly to the visual and olfactory cues, Sumner et al. 1994), and small males which, being slow to arrive and smaller, find it difficult to penetrate the wall of courting suitors (Baird 1968; Parzefall 1973, 1979). Fertility advertisement thus confers two benefits to a female: increasing male-male competition guarantees her access to a superior mate at the peak of her fertile period and at the same time protects her from harassment by less-preferred sneaker males.

Once again, further research introduced new complexity to the story. Substantial variability in the genes responsible for age at maturity, in conjunction with environmental influences (e.g., salinity, temperature) produce marked interdemic variation in male body size (Trexler & Travis 1990; Trexler et al. 1990) and this, in turn, sets the stage for male mating tactics to develop in a relative rather than absolute way. This is apparently what is happening across populations of the Sailfin Molly. Detailed analyses of six allopatric populations in Florida indicated that courtship and gonopodial thrusting rates were not correlated as tightly with male body size as previously thought (Ptacek & Travis 1996). A male's ability to adopt a particular tactic is apparently context dependent. So, if you are a largish small male in a population of large males, sneak, but if you are the same male in a population of small males, court. Hence, the selection vectors, including predation pressure, density, and operational sex ratio, must be incorporated into any discussion about the evolution of alternate male mating tactics in these fish, and possibly, in poeciliids in general.

In yet another poeciliid group, the mosquitofishes (genus *Gambusia*), sexual selection operates in the absence of striking dimorphism in courtship-based traits. In the Eastern Mosquitofish (*Gambusia holbrooki*) most males are monochromatic, like females, but a small percentage of males (about 1.6–7.1%, Regan 1961) display Y-linked black (melanin) speckling (Angus 1989). Speckling appears more conspicuous in open water (Martin 1977), something for which females of other poeciliid species show a strong preference (Kodric-Brown 1985; Houde 1987, 1988). All male mosquitofishes generally use a forced copulation strategy (Itzkowitz 1971; Martin 1975), so intuition suggests that females have no opportunity for mate assessment and are just making the best of a bad situation. Some researchers, however, reported that females demonstrate a bias either for or against speckled males in a simple choice test (Martin 1977; Nelson & Planes 1993; Karplus & Algom 1996; Gould et al. 1999). Similar results were found for the Western Mosquitofish (Taylor et al. 1996b), indicating that they can discriminate based on at least one and possibly more male-based traits in the laboratory. Females also showed a bias toward exaggerated male traits they had never previously encountered, including black fins, an all-black body, and enlarged dorsal or caudal fins. These preferences, measured by presenting the females with models, were not equivalent. For example, females preferred a male with black fins over a normal male, and an all-black male to a black-finned one (Gould et al. 1999). The question now is whether they can act on that ability under more natural situations. The answer to this question appears to be: yes with limitations. Large males dominate small males in agonistic encounters, forming transitory dominance hierarchies around females. The female is not, however, a passive member of the group. She actively spends more time near the dominant male, which, for his part, attempts significantly more copulations than the smaller males in the group (McPeek 1992). Female Western Mosquitofish also spent more time near larger males and even signaled their choice by directing more arches toward their chosen mates (arches may facilitate the gonopodial thrust, Liley 1966; Hughes 1985ab).

The complexity of the mosquitofish system is delineated in the most detail for a population of Eastern Mosquitofish introduced to Italy at the beginning of the 20th century. As is the general case across the Poeciliidae, females in this population flee from males outside of their receptive period; however, male-deprived and postpartum females, both of which presumably have depleted sperm stores, switch their behavior from flee males to approach males. This switch is not a random one. When given a choice, females approach larger males, non-speckled males, and males in a group of three rather than just a single suitor (Bisazza et al. 1998, 2001). Approaching behavior, in turn, is correlated with insemination success; success fell from 90% to 35% as male-deprivation time decreased from 2 months to 15–30 days, so female approach and subsequent behaviors clearly facilitate male insemination even in the absence of courtship. As in the Florida population, males surrounded females in groups of ≤5 in which the largest male guarded the female, blocking mating attempts by his rivals (Bisazza & Marin 1988). Males evidently use visual cues (the absence of the anal spot) to identify postpartum females, and preferentially surround the larger female (Bisazza et al. 1989). Females, for their part, promoted guarding by following the largest male closely (Bisazza & Marin 1991; Dadda et al. 2005). Guarding protects the female from intense harassment, which interferes with foraging, increases predation risk, and may even damage the female if she is subjected to too many forced copulation attempts (Constanz 1984; Pilastro et al. 2003). Females can also reduce the effects of harassment by foraging with other females, the more the better (Dadda et al. 2005). In this case the dilution effect, which is usually used as an anti-predator strategy, provides the same benefits, functioning as an anti-forced copulation strategy. Staying close to a large, guarding male requires that a sneaker will have to be quick, coordinated, and small in order to successfully inseminate the females. The smaller the male is relative to the female, the better he is at hiding in her visual blind spot, and the more successful he is at performing the quick twist-thrust-flee sequence that denotes a successful sneak insemination (Hughes 1985a; Bisazza & Marin 1995; Pilastro et al. 1997). Overall, then, contrary to expectations, female mosquitofish appear to control male mating success to some degree by shoaling with other females, directly selecting large-bodied males, and, as an outcome of male behavior, indirectly selecting only superior sneakers as fathers. The mating system may be dominated by male coercion, but it is not totally determined by it.

High levels of multiple paternity occur in individual broods of mosquitofish (Zane et al. 1999), which sets the stage for intense sperm (male) competition. Unlike the situation documented in the Bluegill, no correlation exists between sperm quality (sperm length, speed following activation, viability, longevity, size, and dissolving rate of sperm bundles) and male body size (except that as noted larger males produce more sperm absolutely, Locatello et al. 2008). Given that all sperm are equal, one way that males can affect their fertilization success is to increase their ejaculate expenditure (increase size of the ejaculate) to offset the impact of multiple inseminations as competition for a female increases (given the physiological ability to make such adjustments, Parker et al. 1996, 1997). Does this in fact happen? Such a dynamic has been demonstrated for Threespine Sticklebacks, in which males adjust ejaculate size and courtship length according to the size and courtship status of a rival, such that a larger ejaculate and shorter courtship occur if the rival is large, and a larger ejaculate occurs if the rival is courting (Zbinden et al. 2001, 2003, 2004). To test the model, wild-caught Eastern Mosquitofish males were placed in one of two situations: four females / no male competitor (low risk, male heaven) and three females / one male competitor (high risk). In the control groups (males were not allowed to mate), high-risk males, as predicted, produced more sperm than their low-risk counterparts (in this case, perception of competition was responsible for an increased rate of spermiation). When males were allowed to interact with females, high-risk males had a lower number of sperm/ejaculate at the end of the trial than did low-risk counterparts, again, also as predicted. The next question is vitally important: Did the males adjust the size of their ejaculate (more sperm when challenged), or did they adjust their behavioral intensity in response to the competitive challenge? The answer was intriguing and unexpected: high-risk males performed more mating attempts, which implies that their reduced sperm count was a result of the simple fact that they mated more often (i.e., they did not invest more in each encounter, they just increased their encounter rate). Even more unexpected was the discovery that there was no difference in the sperm retrieved from females (= successful mating attempts) in the high- and low-competition groups. So, what distinguished a successful male? The answer was straightforward: males who attempted more copulations in either group increased their likelihood of insemination, but few males actually inseminated their partners. Given the decrease in sperm over time in both treatments, this implied that males in general waste sperm during gonopodial thrusts. Video analysis did indeed document the release of sperm packets into the water. The question now becomes, is sperm loss the result of interrupted/incomplete transfer (and if so, which partner created the problem?), or did the females actively reject particular males' sperm after the forced copulation (Evans et al. 2003)?

Multiply inseminated female Western Mosquitofish are larger than singly inseminated ones (Greene & Brown 1991; see also the Southern Platyfish, *Xiphophorus maculatus*, and the Variable Platyfish, *Xiphophorus variatus*, Borowsky & Kallman 1976; Borowsky & Khouri 1976; some populations of Sailfin Molly, Travis et al. 1990; Trexler et al. 1997). Three explanations are possible, operating independently or in any combination, for this difference: larger females, which are older, have had more chances to store sperm; males court large females preferentially because fecundity is tied to female size (Farr & Travis 1986; Travis & Trexler 1987; Bisazza et al. 1989; Travis et al. 1990; Trexler et al. 1997); and large females outcompete small ones by blocking their access to males (Foran & Ryan 1994). This is the point at which behavior overlaps with speciation. Large females are more likely to store sperm from many different males, thus producing more genetically diverse offspring and increasing the potential adaptability of those offspring as a group (Chesser et al. 1984; Brown 1987; but see Meffe 1990). They are also more successful colonizers than males (Brown 1985, 1987; Robbins et al. 1987). These two behaviors lead to increased chances of range expansion, and thus the probability of participating in a vicariant event or establishing a peripheral isolate population, both of which establish geographic disjunctions, setting the stage for speciation.

A Final Word about Sperm

The freshwater environment is not a hospitable one for sperm. The dramatic change in osmolarity between the testis and the hypotonic exterior environment initiates sperm motility while causing damage that may decrease the longevity of individual spermatozoa (Billard 1978; Morisawa 1994; Takai & Morisawa 1995). Evolution has solved this problem in a number of different ways, the most obvious of which was the origin of internal fertilization. A second intriguing mechanism for sperm preservation falls somewhere between internal and external fertilization (Elofsson et al. 2003a). When sperm from Threespine Sticklebacks from fresh water or brackish water are placed in fresh water, they develop knots or blebs along the flagella, which limits their motile period to 30–60 s (comparable to motile periods in fresh water recorded for Salmonidae, Morisawa et al. 1983b; Cyprinidae, Morisawa et al. 1983a; Lahnsteiner et al. 1996; Percidae, Lahnsteiner et al. 1995). Threespine Stickleback males, however, do not spawn like minnows (release sperm in a diffuse cloud, which eventually settles over scattered eggs). They ejaculate close to a compact mass of eggs deposited by the female, eggs that are covered in a thick coating of ovarian fluid. The spermatozoa are thus in contact with fresh water for only a brief period, presumably long enough to be activated, before becoming immersed in ovarian secretions. When such fluids are added to test waters, the Threespine Sticklebacks' sperm motility period is extended from 60 s to an astounding maximum of 7 h (see also Arctic Charr, increased longevity from 43 to 128 s, percentage motility, swimming speed, and linearity of movement, Turner & Montgomerie 2002; Urbach et al. 2005 and references therein). Fishes that spawn in this manner have managed to counteract some of the sperm-damaging effects of hyposmotic shock by, in effect, moving part of their internal environment outside their body. The origin of such semi-external fertilization may explain why some species, but not others, were so successful at colonizing freshwater habitats from the marine environment (Elofsson et al. 2003ab).

The effect of ovarian fluid on aspects of sperm quality has yet to be added to the sperm balance sheet for kleptogamic versus territorial males. The majority of studies discussed previously examined sperm motility and longevity by placing spermatozoa in either a saline solution (e.g., sodium chloride–potassium chloride) then adding lake water or in lake water alone. It will be interesting to determine whether the addition of ovarian fluid will affect all sperm types equally, or whether it will have a differential effect on the sperm from males practicing different mating tactics. Even if no differential response exists, the mating advantage of dominant males possibly arises, in part, from their close proximity to the female during spawning. In effect, their sperm would exploit the positive influences of ovarian fluid, enhancing fertilization success even more over rivals ejaculating at a greater distance or seconds later (Liley et al. 2002).

What about Alternative Female Tactics?

The majority of research on alternative reproductive tactics has focused on male behavior. What about females (for an excellent discussion of this question more broadly defined, see Henson & Warner 1997)? Although cuckoldry was rare in a nearly monogamous population of Largemouth Bass, most sneak spawnings were due to a bonded female spawning with another female's mate (DeWoody et al. 2000b). Research on birds has revealed a substantial amount of infidelity within monogamous species (Griffith et al. 2002), much of which is precipitated by females actively courting passing males whose status is higher than that of their own mates (when their mates are away engaged in territory defense). Such sit-and-wait infidelity is unlikely to occur in fishes because the territorial male probably does not lose sight of his mate in the territory for long periods. Female cuckoldry in a biparental or female-care-only system must therefore involve the female leaving her territory for brief periods of time. How prevalent is female cuckoldry? Is there a female equivalent of a sneaker male, i.e., a nonterritorial female who preys on a nest-holding female by rushing in during the spawning bout and releasing eggs? So many questions remain to be answered.

The search for answers to these questions must include the possibility that females do not play by the same rules as males and thus should not be evaluated by the same criteria. For example, consider agonistic interactions. Aggression can be dangerous to both the aggressor and the recipient if carried to extremes. Evolution has solved this problem in many species by packaging aggressive intent in ritualized displays (e.g., the broadside swim of many fishes) that allow combatants to assess each other's size and skills (resource holding potential, or RHP, Parker 1974) before making the decision to escalate to the more damaging interaction of fighting. Models of such rules of engagement predict that the intensity of combat will increase as the combatants are more and more evenly matched for size, the prime determinant of RHP (e.g., Enquist & Leimar 1983). This is generally what occurs in nature. Male Rio Grande Cichlids, *Herichthys cyanoguttatum*, follow the rules of engagement quite obediently when competing for a territory containing a clay flowerpot, coveted by lab-confined cichlids as a nesting site. The largest male always wins and ties almost always occur when size asymmetry is minimal. Female Rio Grande Cichlids join their partners in territorial defense and show the full range of male agonistic behaviors. Although they competed as intensely as males for flowerpots, size was not a good predictor of success. In 18% of the contests the smaller female was victorious (even ≤54% asymmetry in size), and ties (22% of contests) were unrelated to asymmetry. Females may be motivated directly by the value of the resource, so the more valuable the flowerpot was to an individual, the more willing she was to escalate an aggressive interaction. Why might the same resource have different values for individual females? The most obvious explanation in fishes is that resource value will change with the ovulatory cycle, so the closer a female comes to ovulation and the danger of losing an entire clutch if an appropriate spawning site/mate (resource) is not found, the more valuable that pot or male becomes to her. Thus a small, ovulated female can defeat a large female who is still in the interspawning interval (Draud et al. 2004). Resource value is clearly more difficult to measure than size, so investigations of this fascinating idea will require some creative thinking by researchers.

WHEN GOOD LOVING GOES BAD: HYBRIDIZATION AND INTROGRESSION

> Reproductive compatibility is an attribute of the members of the ancestral species, which is gradually diminished and ultimately lost.
>
> (Rosen 1979:277)

Biologists are quite successful at creating hybrids between numerous North American freshwater fishes in the laboratory (reviewed in Bartley et al. 2001), indicating that many fishes have the potential to hybridize when given no other choice (or when the hybrid is produced from hand-stripped eggs and sperm). The fact that some species make mating mistakes under the uniform conditions in a laboratory does not necessarily indicate that such mistakes will be widespread in the wild. Many closely related species show differences in environmental preferences (breeding temperature, substrate, water velocity) and mating behaviors, which decrease the probability that they will come into contact even when they are geographically overlapping or they will recognize one another in the presence of conspecifics. Bearing this in mind then, how often is the potential to hybridize realized in the wild? The answer to this question is: surprisingly often (e.g., Scribner et al. 2000).

Natural Mistakes Favor the Formation of Hybrids

Hybridization events may occur naturally as the outcome of particular life history traits. For example, the sperm of the Logperch (*Percina caprodes*) remains viable in water longer than sperm from the Orangethroat Darter, allowing chance intergeneric hybridization when the Logperch is sympatric with other darters (Hubbs 1957). Similarly, Largescale Suckers (*Catostomus macrocheilus*) and Bridgelip Suckers (*Catostomus columbianus*) may hybridize because both their spawning times and preferred spawning habitat overlap, creating the possibility for accidental fertilization during the frenzied spawning aggregates that form the basis of the Sucker breeding system (Dauble & Buschbom 1981).

The most widespread life history trait associated with natural hybridization events, especially in cyprinids, is the propensity to spawn over another species' nest (Figs. 2.14–2.15). At least 44 cyprinids are nest associates, the preferred host usually being another cyprinid (Johnston & Page 1992; Table 2.4). In most cases, such association and resultant hybridization appears to be a result of chance (the host species just has the bad luck of nesting in the wrong place at the wrong time, e.g., Raney 1947; Lachner 1952; Cooper 1980) in combination with environmental change. For example, the Blackside Dace (*Chrosomus cumberlandensis*) and Tennessee Dace (*Chrosomus tennesseensis*) spawn over clean gravel patches in the tiny headwater streams where they live (Starnes & Starnes 1981; Starnes & Jenkins 1988). Degradation of those streams via human activities in residential areas, or silt-laden runoff from coalmines, may have forced the dace into close contact with Creek Chubs (Eisenhour & Piller 1997). Creek Chubs are larger (by about 6–9 mm on average) than either dace in the areas of overlap, so the dace may simply be outcompeted for access to limited spawning sites, and use nest association as an alternate strategy (i.e., they may be facultative nest associates). This example supports Hubbs's (1955) insight that reduction in suitable spawning sites due to habitat alteration would increase the likelihood of hybridization by forcing previously segregated species into contact with one another.

Pushing a Plesiomorphic Button

The ability to make mating mistakes exists in many, if not all, breeding systems. In some cases, a species may retain the capability to perform a plesiomorphic behavior, but that capability is normally suppressed. For example, in laboratory studies, two egg-clumping fishes, the Johnny Darter (*Etheostoma nigrum*) and the Stippled Darter (*Etheostoma punctulatum*), reverted to the plesiomorphic behavior of burying their eggs when denied appropriate substrate (Page & Simon 1988). The central nervous system is extremely conservative in vertebrates, in part because neurons are generally multifunctional and part of numerous pathways. Selection against obsolete pathways is thus more likely to take the form of inhibition or suppression of particular components, rather than actual physical loss (Kavanau 1990). Under certain circumstances—e.g., changing environmental conditions (absence of appropriate habitat or mates)—the block is removed and previously inaccessible circuitry is activated, releasing the plesiomorphic (or relictual) response.

In other cases, the mistake may be the result of signals from heterospecifics triggering a plesiomorphic behavior in an inappropriate context. The trigger may be activated following environmental disturbances, particularly those that interfere with effective transmission of mating signals. It also may be activated if one species is rare relative to another (e.g., Hubbs et al. 1943ab; Hubbs & Hubbs 1947; Hubbs & Miller 1953; Stevenson & Buchanan 1973; Tyus & Karp 1990). Such density disparities may exist along the edges of species ranges, in dispersal corridors used to move between habitat patches (e.g., Douglas & Marsh 1998); have occurred in the past as some fish species began dispersing out of refugia, following the retreating glaciers (Hubbs 1955); be the result of one species suffering a decrease in population size based on factors that have not affected the more abundant taxon (e.g., through habitat degradation); or be the result of non-native introductions into an area for biological control, stocking rivers and lakes for recreational fishing, through connection of previously separate drainages, or stream capture followed by range expansion (Allendorf & Leary 1988; Echelle 1991; DeMarais & Minckley 1992; Koppelman 1994; Bestgen & Propst 1996; Rosenfield 1998; Grant et al. 2002b). In these situations, individuals from the less frequent taxon may simply find themselves swamped by the courtship signals of the other species (Hubbs 1955). If these individuals share some plesiomorphic aspects of their mate recognition system, then they will make mistakes, presumably in relation to the amount of plesiomorphic overlap existing between the two species. For example, Jennings and Philipp (2002) suggested that widespread hybridization among Sunfish species occurs in the face of strong mate discrimination (Keenleyside 1967; Steele & Keenleyside 1971) because males tend to sneak fertilizations in adjacent nests (e.g., introduced male Redear Sunfish, *Lepomis microlophus*, nested among native Longear Sunfishes, refused to court Longear Sunfish females, even though conspecific females were rare, but could not resist the temptation to intrude on their neighbors' courtship interactions).

Results of Hybridization

A successful hybridization event has three possible outcomes (see discussion by Avise 2001; Brooks & McLennan 2002 and references therein). First, the two lineages may merge (e.g., Matthews et al. 1982b). Depending on the extent of contact, the two lineages may disappear completely as independent entities (producing one variable species), the two lineages may merge only in the area of overlap (hybrid zone) but remain independent in areas of allopatry, or the lineage with a limited distribution may be swamped by the more widespread lineage. Second, the two lineages may complete speciation after secondary contact (speciation by reinforcement, Dobzhansky 1937; alloparapatric speciation, Endler 1977). The expected outcome of this dynamic is the production of a hybrid zone that should decrease over time following the enhancement of mate recognition signals and gradual production of two distinct species. Finally, the two lineages may merge partially to form a hybrid species, which remains distinct from the parental species (reticulate speciation). The hybrid may exhibit some or all of the apomorphies of both parental species, making studies of mate recognition particularly fascinating.

Here, I focus on the third outcome, the formation of hybrid species. Occasionally, hybridization disrupts meiosis, producing self-perpetuating unisexual (female: gynogens) lineages with an F_1 phenotype (Muntzing 1940; Schultz 1969; Dawley 1987; Vrijenhoek 1989; Goddard & Schultz 1993). At present three such hybrid species are known in the fresh waters of North America. I discuss two of them. For a discussion of the third, the complicated Northern Redbelly Dace (*Chrosomus eos*) × Finescale Dace (*Chrosomus neogaeus*) system, see Goddard et al. (1989).

Amazon Mollies, *Poecilia latipinna* × *P. mexicana* = *P. formosa*

Mollies are small, livebearing fishes living in habitats from the southeastern United States to northern South America. The aptly named Amazon Molly (*Poecilia formosa*, Hubbs & Hubbs 1932; Fig. 2.16) is the unisexual byproduct of a single mating mistake between a female Shortfin Molly and a male Sailfin Molly (Fig. 2.2) (Hubbs 1955; Abramoff et al. 1968; Turner et al. 1980; Turner 1982; Avise et al. 1991) about 120,000 generations ago near Tampico, Mexico (Schartl et al. 1995; for an extensive discussion of this system, see Schlupp 2009). The outcome of this mistake was the production of diploid gynogens. Female gynogens actively court and mate with males whose sperm triggers embryogenesis (Schlupp 2005) but is generally not incorporated into the embryo (rare fertilization events produce triploid individuals). Every time a male mates with a gynogen, he is wasting sperm, time, and energy, and increasing his risk of predation because of decreased vigilance. Why do males continue to make such an egregious fitness mistake? The answer to this question involves the evolution of two things: the female signal and the male response.

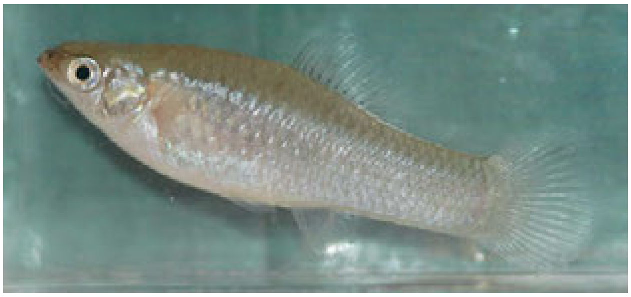

Figure 2.16. The Amazon Molly, *Poecilia formosa*, is an all-female species that arose from a cross in the wild between a female Shortfin Molly, *Poecilia mexicana*, and a male Sailfin Molly, *Poecilia latipinna* (see Fig. 2.2) >120,000 generations ago (individual captured in the Rio Tigre, near Aldama, Tamaulipas, Mexico, September 2007; photograph by and used with permission of Michael Tobler).

The Amazon Molly inherited components of both parental species' mate recognition system from the original hybridization, so gynogenetic females should be transmitting at least some plesiomorphic cues to surrounding males. Because daughters are asexual clones of the female involved in the initial hybridization, evolution of those cues via the accumulation of genetic change and selection will happen slowly. Indeed, few behavioral differences have been documented between Amazon Mollies and either Sailfin Mollies or Shortfin Mollies (Schlupp 2009). The female part of the male-female dialogue would thus appear to have remained relatively static since the origin of the Amazon Molly (frozen-mate attraction hypothesis, Lima et al. 1996; the females represent a frozen F_1, Dries 2003). Has the male response to the putative plesiomorphic cues also remained static?

Initial studies indicated that male abilities to discriminate between conspecific (sexual) and gynogenetic females was dependent on whether the test males were collected from populations that were allopatric to, or sympatric with, Amazon Mollies. In general, males from populations sympatric with gynogens demonstrated a stronger attraction to conspecific females than did males from allopatric populations (Hubbs 1964; Ryan et al. 1996;

Gabor & Ryan 2001). Closer examination revealed an even more complicated picture; male response was based on an interaction between visual cues conveying information about species identity (the exact cue is unknown) and about fecundity (female body size). So far, two different outcomes have been detected (Gumm & Gabor 2005; Gabor et al. 2010): a balance between the two preferences in one sympatric population (no choice between large gynogens and small conspecifics) and one allopatric population (no choice between large gynogens and small conspecifics; preference for conspecific when females are size matched, Gabor & Ryan 2001; and a shift toward a preference for medium-sized females in one sympatric population, prefer smaller conspecific over larger gynogen). Add olfaction into the mix and the complexity of the male-female dialogue increases: males spend more time near the fertile female (fertility advertisement) regardless of her species (Schlupp et al. 1991). Males also copy each other, so preference for a conspecific can be overridden by seeing another male courting a gynogen (Schlupp & Ryan 1997). More importantly, female mollies, like many poeciliid species, copy each other's mate choices, so males might actually get some benefit by mating with a gynogen if it attracts conspecific females (Schlupp et al. 1994; Heubel et al. 2008). Sexual females, however, appear to evaluate the quality of the model, copying the choices of conspecifics more intensely than those of gynogens (Hill & Ryan 2006), so such benefits are expected to vary across populations, depending on the frequency of sexual and gynogenetic females.

Overall, the fact that the Amazon Molly has persisted over 120,000 generations represents the outcome of an interaction among mate choice and natural history parameters (e.g., the density of gynogens). The interaction is a dynamic one; Sailfin Mollies (Fig. 2.2) dominate in some populations, but gynogens dominate in others. For example, a recent census of habitats around Brownsville, Texas, indicated that the ratio of Amazon Mollies:Sailfin Mollies had changed dramatically from advantage gynogen (4.2 times more abundant, Hubbs 1964) to advantage Sailfin Molly in 7 of 10 sites (McNeely & Wade 2003). The reasons for this dramatic shift are currently unknown but perhaps were influenced by a variety of habitat alterations, including increased turbidity (Heubel & Schlupp 2006), decreased aquatic plant diversity (male preference for conspecific versus gynogenetic females is weakened as threat of predation increases, Aspbury et al. 2010b), the introduction of Blue Tilapia (*Oreochromis aureus*) (McNeely & Wade 2003), and the fact that Amazon Mollies are less tolerant of cold temperatures (selective winter mortality, Fischer & Schlupp 2009) and are more susceptible to food stress (Tobler & Schlupp 2010) than are Sailfin Mollies.

Males from a third species, the Tarnesi Molly (*Poecilia latipunctata*), were identified as suitable sperm donors for Amazon Mollies. The dynamics are similar to those described for other donor species; the males are clearly more attracted to conspecific females, yet they make mistakes, albeit at low levels under laboratory conditions (Niemeitz et al. 2002). The Tarnesi Molly has a restricted range and is classified as threatened (Tobler & Schlupp 2009). Until the recent construction of interconnected irrigation ditches, it rarely came into contact with gynogens (Darnell 1962). Will this change have a negative impact on the Tarnesi Molly, contributing to its progress from threatened to endangered, or even extinct? The answer will depend on a number of factors, including how often Tarnesi Molly males pursue and mate with gynogens, whether there are any benefits to the male counteracting such mating mistakes (e.g., through female mate copying as discussed previously), and whether Amazon Molly females themselves only actively court Tarnesi Molly males when the Shortfin Molly is unavailable.

Bisexual-Unisexual System, *Poeciliopsis monacha* × *P. lucida* = *P. monacha-lucida*

Poeciliopsis monacha (Headwater Livebearer) is a small live-bearing topminnow inhabiting ephemeral headwater springs and arroyos in northwestern Mexico (Miller 1960). Fish in these habitats are subjected to seasonally fluctuating temperatures, from <12°C in the winter to >40°C during the dry season with corresponding differences in dissolved oxygen. The species is genetically polymorphic with at least some of the alleles related to differences in survival under these harsh environmental conditions (Vrijenhoek et al. 1992). Mismatings between female *Poeciliopsis monacha* and male *Poeciliopsis lucida* (Clearfin Livebearer) produce two types of gynogens, both of which court and attempt to mate with *P. lucida* males. Diploid gynogens produce haploid eggs carrying only the *P. monacha* genome. Although incorporated into the zygote, the genetic complement of the sperm is never incorporated into the daughter's eggs, which carry only the maternal genome (Schultz 1966, 1969; Cimino 1972a; Vrijenhoek 1972). The union of a diploid egg and haploid sperm produces triploid females (Schultz 1967; Cimino 1972b). Depending on the species of the father, these triploid hybrids are either *P.* 2 *monacha-lucida* or *P. monacha-2 lucida*. These complicated reproductive iterations produced many hemiclonal lineages within and between populations (Vrijenhoek et al. 1978; Angus & Schultz 1979). Unlike the Amazon Molly, the *Poeciliopsis* clonal lineages are hypothesized to have arisen from multiple hybridization events (Angus & Schultz 1979; Vrijenhoek 1979, 1984; Wetherington et al. 1989; Weeks & Gaggiotti 1993), forming a hybrid species complex since more than one independently derived, self-perpetuating lineage occurs within the group (Frost & Wright 1988; Echelle et al. 1989b; Echelle 1990; see also the North American marine gynogenetic system, *Menidia clarkhubbsi*, Texas Silverside, Echelle et al. 1983, 1988, 1989a).

Just as in the *Poecilia latipinna* system, male *Poeciliopsis lucida* prefer conspecific females to the gynogens, but this preference appears to be partly based on learning (McKaye 1971; Moore & McKaye 1971). Males also appear to have a preference hierarchy among the different gynogenetic lineages. When males discriminated, they showed a significant preference for clonal females that looked different from the clones they were raised with. They did not always discriminate, possibly because they could not distinguish among all lineages, many of which looked superficially similar to a human observer (Keegan-Rogers 1984). If discrimination is based on learning during early development, then a continual fluctuation of different morphologically and chemically distinct clonal lines will make it more difficult for males to generalize from their early experiences across all novel females they encounter. In effect, the shifting frequency of gynogenetic lineages acts like the shifting surface antigens used by schistosome parasites to confuse the hosts' immune system.

These clonal lineages provide an excellent system for studying the genetic basis of behavior. For example, *Poeciliopsis monacha* females are extremely cannibalistic, but *P. lucida* females are not. Not surprisingly, *P. monacha* fry tend to avoid their mothers by hiding near the substrate, while *P. lucida* fry swim quite unperturbed beside their mothers (Lima & Vrijenhoek 1996). The percentage of cannibalism within the clonal lineages can be arranged in series according to the proportion of the genome that was contributed by *P. monacha*: *P. monacha* (100%) > MML (*P. 2 monacha-lucida* triploid: 88%) > ML (*P. monacha-lucida* diploid: 74%) > MLL (*P. monacha-2 lucida* triploid: 12%) > *P. lucida* (0%) (Thibault 1974). Fry avoidance behaviors roughly parallel the changes in cannibalistic tendencies, although the changes are not as striking and are confounded by fry size at birth (Lima &Vrijenhoek 1996). Cannibalism, particularly of your own offspring, is difficult to understand within an evolutionary framework (review by FitzGerald 1992). Is it just a mistaken byproduct of predatory behavior (Lima & Vrijenhoek 1996), a way to hedge bets by sacrificing some current reproductive success (using offspring as food to enhance condition) for potential success in the future (Rohwer 1978; Sargent 1992), an artifact of laboratory conditions (Schenck & Vrijenhoek 1989; Weeks et al. 1992), or simply maladaptive? The ability to manipulate both the genetic background and environmental parameters in the *Poeciliopsis* clones provides an elegant system for testing these hypotheses as well as for studying the evolution of fry counterstrategies to parental cannibalism in what may well be a parental-offspring evolutionary arms race.

Hybridization: A Summary

Hybridization appears to happen quite often in North American freshwater fishes, but most species manage to maintain their own integrity (Whitmore 1983). In areas of widespread hybridization, introgressive swamping is generally rare because the hybrids (F_1s, F_2s, and backcrosses) display an abnormal sex ratio, have reduced fertility or viability, or are at a selective disadvantage (e.g., Dowling & Moore 1984, 1985ab; Allendorf & Waples 1996; Hawkins & Foote 1998). In some instances, however, gene flow from one species to another occurs without the loss of species integrity. Limited introgression may increase genetic variability in a species and thus increase the scope for selection and drift in combination with geological factors to produce distinct lineages (Anderson 1953; Lewontin & Birch 1966; Barton & Hewitt 1985; Slatkin 1987; Rhymer & Simberloff 1996). So hybridization may be an essential part of species diversification in some lineages (Verspoor & Hammar 1991; Dowling & DeMarais 1993). The implications of such a mechanism are not trivial because it will affect how we measure the cost of the initial mating mistake to the erring fishes. Introgression also may be a negative force in some interactions. For example, Rhymer and Simberloff (1996) wrote that introgression was thought to play a contributing role in 3 of 24 extinctions of animal species in North America. Those three species were all fishes: the Tecopa Pupfish (*Cyprinodon nevadensis calidae*), Amistad Gambusia (*Gambusia amistadensis*), and Longjaw Cisco (*Coregonus alpenae*) (McMillan & Wilcove 1994).

CONCLUSION

Mate recognition is always a complicated process, involving information transfer between prospective mates and from the courting pair to interested bystanders (other conspecifics and predators). Tinbergen (1948, 1951, 1952) was the first ethologist to delineate the complexity of this interaction. His painstaking descriptions of stimulus (signal)-response (countersignal) chains in the courtship of Sticklebacks (among other animals) highlighted not only the sophistication of information transfer in these fish, but the importance of that information for mate recognition and selection and for synchronization between partners. In North American freshwater fishes these chains are forged with visual, chemical, tactile, near touch, and acoustic links (the importance of communication based on electrical fields has not yet been explored in any detail), creating a multidimensional mate recognition template.

New researchers interested in studying the evolution of mating behavior in North American freshwater fishes can expect to encounter many joys and frustrations in their search for a viable system. On the positive side, generations of ichthyologists have created a large database comprising meticulous descriptions of behavior and life history traits. Many of those species, however, have not been subjected to rigorous experimental examination of the evolutionary forces involved in shaping mating behaviors, so the field is relatively wide open for newcomers. Enhanced video technology allowing us to peer voyeuristically on spawning fishes in the field is revealing unexpected information. How many incorrect hypotheses were erected before it was discovered that the bizarre jugular position of the urogenital opening in the Pirate Perch (*Aphredoderus sayanus*) allows individuals to deposit gametes deep within channels through underwater root masses, where developing embryos are protected from fast-flowing currents, predators, and siltation (Fletcher et al. 2004)? On the negative side, most experimental attention has focused on only a few members of a clade (centrarchids, gasterosteids, and poeciliids are the most obvious species-ist clades) or on only one sex. In systems for which we have adequate observational and experimental data, we tend to know little about the mechanisms underlying behavioral expression. Is it genetically controlled to any extent? What is the role of hormonal control of its development and expression? How do the sensory and neural systems involved in detecting and processing the behavioral signal operate? What effects have the transmission properties of the environment had on shaping that signal? What role does learning play, if any, in the system? As a result we have a well-developed database about the evolution of mating behaviors for only a small fraction of North American freshwater fish diversity (for discussion of this problem vis-à-vis imperiled fishes, see Johnston 1999).

Behavior is a critical component in the production of that diversity. All nonallopatric modes of speciation are ultimately dependent on individuals maintaining genetic distinctiveness by mating assortatively. Although vicariant speciation does not require the evolution of unique mating behaviors, a population exposed to a new selective regime in a novel habitat may respond with adaptive shifts in ecology and morphology and in mate-recognition characters, forming a unique mate-recognition system (Paterson 1985). The diversification of mating behaviors is thus linked causally to the production of diversity. The corollary is that the retention of plesiomorphic mating characters may be responsible for the loss of diversity under some conditions. For example, introductions of non-native species can intensify competition for limited spawning sites or increase the probability of interspecific mating mistakes and subsequent hybridization. Even if introgression is limited, such hybridization may wreak havoc on species with limited distributions and low population diversity (Hubbs 1955). Models simulating the impact of introgressive hybridization have demonstrated that extinction rates for parental taxa can be quite rapid if one of the taxa is rare, and if assortative mating is weak initially, or weakened due to habitat degradation (Epifanio & Philipp 2001).

Habitat degradation includes more than just loss of spawning sites, forcing heterospecifics into closer and closer associations, and thus increasing the probability of hybridization either via chance (e.g., nest associates) or actual mating mistakes. The efficiency of courtship communication is directly dependent on the transmission properties of the medium. Anthropogenic intervention can disrupt breeding systems by operating on those transmission parameters. For example, noise from boats or hydroelectric dams contains low-frequency components, overlapping the transmission and detection frequencies of many freshwater fishes. This interference may damage a fish's hearing abilities in the long term (something akin to attending too many rock concerts in quick succession), and disrupt courtship communication in the short term (e.g., Scholik & Yan 2002ab). The olfactory system is exposed directly to the environment and thus extremely susceptible to damage by dissolved pollutants (e.g., copper, lead, mercury, nickel, zinc, silver, cadmium) (Saucier & Astic 1995; Beyers & Farmer 2001 and references therein; Scott et al. 2003; Sloman et al. 2003) and organophosphates (Moore & Waring 1996b, 2001; Waring & Moore 1997). Of direct relevance to North America is the demonstration that relatively minor acidification of holding waters (from pH 7.0 to 6.0), eliminates the response to alarm cues in the Fathead Minnow, Finescale Dace (Brown et al. 2002a), Pumpkinseed (Leduc et al. 2003), Rainbow Trout (Leduc et al. 2004, 2008; Scott et al. 2003), Brook Trout (*Salvelinus fontinalis*, Leduc et al. 2004), Iowa Darters (*Etheostoma exile*, McPherson et al. 2004), and Atlantic Salmon (Leduc et al. 2006, 2009), including the fish's ability to learn the scent of a novel predator via coupling the predator's scent with a conspecific alarm cue (Leduc et al. 2004, 2007b). Alarm-based anti-predator reactions are triggered by the hydroxylamine group on the hypoxanthine-3-N-oxide molecule at least in minnows (G. E. Brown et al. 2000). Acidification alters the chemical structure of that trigger (6,8 dioxypurine), eliminating its biological functionality (Brown et al. 2002a). Because acidification damages both the receiver (sensory system, Moore 1994b) and the sender (the cue) its effects can sweep rapidly through the system.

The effects of anthropogenic interference are often complex, affecting mating systems in unpredictable ways. For example, under turbid conditions caused by enhanced phytoplankton growth, female Threespine Sticklebacks paid more attention to courtship intensity (Engström-öst & Candolin 2007) and olfactory cues (Heuschele et al. 2009) than to color signals. Under normal clear water conditions, males adjust their courtship and color intensities based on input from competitors; in general males in good condition dominate their poor-condition neighbors (Candolin 1999, 2000ab). In turbid waters, male-male interactions decreased, relaxing the social control of signal production and allowing poor-condition males to ramp up their color and courtship over the short term. Unfortunately these males generally do not have the energy reserves required to be effective fathers, which makes them a bad choice for any female (Wong et al. 2007; Candolin 2009), at least in normal, clear water. Eutrophic waters, however, decreased territorial interactions during egg and fry guarding (because males are not as visible) and increased oxygen supply to the developing embryos (decreasing the need for pectoral fanning), both of which increased hatching success. In other words, the same environmental perturbation that decreased the honesty of visual signals and thus the effectiveness of mate choice increased the reproductive success of all parental males (Candolin et al. 2008). Equally fascinating, the acidification associated with eutrophication increased the efficacy of olfactory communication (Heuschele & Candolin 2007), which may compensate, in part, for the decreased reliability of courtship intensity cues, assuming that poor-condition males cannot manipulate their scent as well as their behavior and color. Just exactly what these changes will mean to population structure in the long run is something that only time can tell us.

Overall, many fish species appear to be disappearing because of anthropogenic changes (Miller 1961), and many of those changes have a direct effect on the breeding system (see extensive review of the effects of pollution on the reproductive behavior of fishes by Jones & Reynolds 1997). Loss of these species involves more than just adding a name to the IUCN Red List. It involves the loss of all the unique behaviors belonging to that species, which might include tail waggling, popping, purring, zigzagging, jaw locking, gonopodial nibbling, probing, quivering, and broadside swimming. It is thus more crucial than ever that videotapes and sonograms of the behavioral repertoire of as many fishes as possible be deposited in a central repository. We have a small window of opportunity for building such a database because the attention of the general public and funding agencies is drawn to the efforts of systematists to inventory all of the diversity on this planet. Although these inventories often involve collaborations between different systematists, to my knowledge no one studying behavior is participating at any level. Ethological ichthyologists, indeed all ethologists, need to be more proactive about this, both in attaching themselves to ongoing inventories and in packaging their own gold mine of data for storage and public access.

In my experience people who would normally not give much thought to conservation issues become far more interested when they see animals interacting with one another, particularly if that interaction involves courtship and caring for offspring. Of all the animals in North America, the freshwater fishes provide us with the most diverse, bizarre, and entrancing examples of such interactions. We are living in the information age and behavior is fundamentally the transmission and interpretation of information. It is not so surprising then that behavior crosses interspecific boundaries and speaks to us all.

Acknowledgments

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Chapter 3 Petromyzontidae: Lampreys

Ian C. Potter, Howard S. Gill, and Claude B. Renaud

Lampreys (Petromyzontiformes) and Hagfishes (Myxiniformes), which are both scaleless and eel-like in body form (Fig. 3.1), are the sole surviving representatives of the agnathan (jawless) stage in chordate evolution (Hardisty 1982, 2006; Forey & Janvier 1993). The Lampreys comprise 38 species in 10 genera (Potter & Gill 2003), together with the Drin Brook Lamprey (*Eudontomyzon stankokaramani*), which Holčík & Šorić (2004) subsequently recognized as a valid species, and the Western Transcaucasian Brook Lamprey (*Lethenteron ninae*) and the Epirus Brook Lamprey (*Eudontomyzon graecus*) (described by Naseka et al. 2009 and Renaud & Economidis 2010, respectively).

The larva of the Lamprey, which is blind and toothless (Fig. 3.1a), lives in the soft substrates of streams and rivers, where it feeds on microorganisms and detritus (Hardisty & Potter 1971a; Moore & Mallatt 1980). The burrowing behavior of the larva led to it being termed an ammocoete, which means "embedded in sand." After a number of years, the ammocoetes of all species undergo a radical metamorphosis (Potter 1980a; Youson 1980). During this process, the Lamprey develops eyes and a suctorial disc that bears curvilinear (alate) rows of teeth, prominent infra- and supraoral tooth-bearing laminae, and a protrusible tooth-bearing and tongue-like piston (Fig. 3.2). At the completion of metamorphosis, 18 of the Lamprey species move to the wider areas of rivers or to lakes or the sea, where, depending on the species, they spend from a few months to >3 years. In this phase of the lifecycle, they use their suctorial disc to attach to their hosts, which are mainly actinopterygian (Ray-finned) fishes (Applegate 1950; Hardisty & Potter 1971b; R. J. Beamish 1980; Halliday 1991; Renaud et al. 2009a). The teeth on the suctorial disc help Lampreys maintain their position on the host, while the teeth on the tongue-like piston are used to penetrate the host tissue (R. J. Beamish 1980; King 1980; Potter & Hilliard 1987; Renaud et al. 2009a). After a period of substantial growth, parasitic species cease feeding and migrate to their spawning areas in rivers and streams.

In contrast to the 18 parasitic species, the other 23 species reach maturity within a year of completing metamorphosis and do not feed as adults; they are thus termed "nonparasitic species" (Hardisty & Potter 1971c). Nevertheless, these nonparasitic species still develop the armory used by parasitic species for feeding as adults (Bird & Potter 1979a; Holmes et al. 1999). Because the morphology of the metamorphosed individuals of many nonparasitic species closely resembles that of certain parasitic species, each of those nonparasitic species is believed to have evolved from a given parasitic species and thus together they constitute paired species (Hardisty & Potter 1971c; Potter 1980b; Hardisty 2006; Docker 2009). The two main phenotypic features that distinguish the nonparasitic member from the parasitic member of each paired species are a far smaller adult body size and much lower absolute fecundity. All Lamprey species are, however, semelparous (i.e., die after a single spawning season).

In marked contrast to Lampreys, which have a larval phase spent in fresh waters, Hagfishes do not have such a phase and spend their entire life in marine environments (Hardisty et al. 1989; Hardisty 2006). Moreover, unlike Lampreys, which are iono- and osmoregulators, the Hagfishes are iono- and osmoconformers and cannot tolerate fresh water and low salinities (Bartels & Potter 2004; Wright 2007). Indeed, the extant Hagfishes are unique

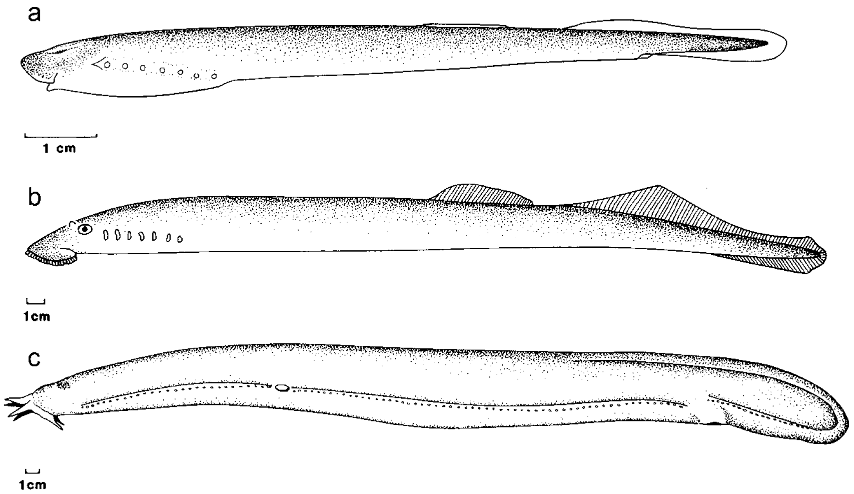

Figure 3.1. Lateral views of (a) larval Lamprey (ammocoete), (b) adult Lamprey, and (c) Hagfish (reproduced by permission of the Royal Society of Edinburgh from *Transactions of the Royal Society of Edinburgh: Earth Sciences* volume 80 (1989), pp. 241–254).

among vertebrates in that their sodium and chloride serum concentrations approximate those of their marine environment with the result that their internal milieu is iso-osmotic with that of their environment. These characteristics imply that Hagfishes have always lived exclusively in marine environments (Lutz 1975). It was thus surprising when a Hagfish, †*Myxineidus gononorum*, was found in reputedly freshwater deposits of the Late Carboniferous (about 318–299 mya) in Allier, France (Poplin et al. 2001).

Because adult Lampreys and Hagfishes share many features, such as an eel-like shape, a tongue-like piston that bears teeth, and gills that are located in pouches, and since both groups lack scales, bone, and paired fins, many taxonomists and comparative anatomists have considered Lampreys and Hagfishes to be closely related. Lampreys and Hagfishes were thus both placed in the class Cyclostomata or Marsipobranchii, which recognizes their possession of round mouths and pouch-like gill sacs, respectively (Hardisty 1979). The roots of the ordinal name Petromyzontiformes mean "stone," "to suck," referring to the attachment by adult Lampreys to rocks during nest building and mating.

After comparing numerous morphological characteristics in extant and fossil agnathans and gnathostomes (jawed vertebrates), and the physiological characteristics of the living Lampreys, Hagfishes, and gnathostomes, several workers questioned whether the two groups of living agnathans are monophyletic (e.g., Hardisty 1979, 1982; Janvier 1981; Forey & Janvier 1993; Forey 1995; Near 2009). Indeed, these comparisons led to the view that Lampreys are more closely related to the gnathostomes than to the Hagfishes. Although a few molecular analyses likewise did not support the monophyly of Lampreys and Hagfishes (Suzuki et al. 1995; Rasmussen et al. 1998), the

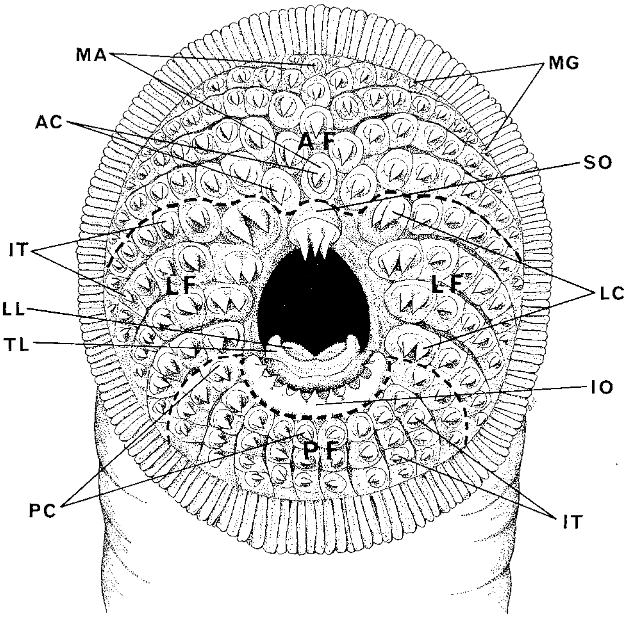

Figure 3.2. Oral disc of the Ohio Lamprey, *Ichthyomyzon bdellium*, showing the different fields and types of teeth and laminae and their nomenclature. Note the alate rows comprising an inner circumoral and an outer marginal, and the intervening intermediate rows of disc teeth. MA, median anterior tooth row; MG, marginal teeth; AF, anterior field; AC, anterior circumoral teeth; SO, supraoral tooth plate; LF, lateral field; IT, intermediate disc teeth; LC, lateral circumoral teeth; LL, longitudinal lingual laminae; TL, transverse lingual lamina; IO, infraoral lamina; PC, posterior circumoral teeth; PF, posterior field (reprinted from *The Biology of Lampreys*, Vol 1, M. W. Hardisty and I. C. Potter, eds., C. L. Hubbs and I. C. Potter, Distribution, Phylogeny and Taxonomy, pages 1–65, 1971).

majority of such analyses supported monophyly of the Cyclostomata (e.g., Stock & Whitt 1992; Mallatt & Sullivan 1998; Kuraku et al. 1999; Delarbre et al. 2002; Takezaki et al. 2003; Blair & Hedges 2005; Kuraku & Kuratani 2006).

In view of marked differences between the evolutionary implications of morphological and molecular data, Near (2009) subjected a combination of phenotypic and molecular data sets for Hagfishes, Lampreys, and gnathostomes to phylogenetic analyses. He showed that the implication that Lampreys and Hagfishes were monophyletic depended on the type of analysis used (i.e., maximum parsimony versus Bayesian), and suggested that strong support for the monophyly of the cyclostomes inferred from molecular data sets should be treated with measured skepticism. While the precise relationships of Hagfishes, Lampreys, and gnathostomes was still hotly debated as recently as 2009 (Janvier 2009; Nicholls 2009), the results of microRNA studies appear to leave little doubt that the cyclostomes are monophyletic (Heimberg et al. 2010; Janvier 2010).

Irrespective of arguments regarding the closeness of the relationship between Lampreys and Hagfishes, the discovery of a well-preserved Lamprey fossil in Devonian deposits (416–359 mya) in South Africa implies that these two taxa have been separated for >360 million years (Gess et al. 2006). Indeed, analyses of cDNA data led Kuraku & Kuratani (2006) to conclude that the two groups of cyclostomes diverged between 470 and 390 mya.

DIVERSITY AND DISTRIBUTION

The extant Lampreys, which comprise three families, have an essentially anti-tropical distribution (Hubbs & Potter 1971). The 37 species of the Petromyzontidae, the Northern Hemisphere Lampreys, live in the cooler waters of North America, Europe, and Asia (see Figs. 3.3–3.8 for the distribution of this family in North America), but the 3 species of the Mordaciidae, the Southern Top-eyed Lampreys, and the sole species of the Geotriidae, the Southern Striped Lamprey, are restricted to temperate regions of the Southern Hemisphere (Table 3.1).

The anti-tropical distribution of Lampreys is related, at least in part, to the inability of ammocoetes to tolerate high temperatures. This is exemplified by the fact that the ultimate incipient lethal temperatures of the Sea Lamprey (*Petromyzon marinus*) from North America, the European Brook Lamprey (*Lampetra planeri*) from Europe, and the Pouched Lamprey (*Geotria australis*) from Australia are 31.4, 29.4, and 28.3°C, respectively, and thus below the temperatures often recorded in tropical rivers (Potter & Beamish 1975; Macey & Potter 1978).

Any description of the diversity and the distribution of Lampreys (Figs. 3.3–3.8) needs to recognize that the biological characteristics and ecological requirements of their ammocoetes and adults differ markedly. This is particularly the case with anadromous parasitic species, where the essentially sedentary and burrowing ammocoete is confined to fresh water and the adult, during its feeding phase, occupies the marine environment in which it can become widely distributed and thus move far outside the geographical range of its larval phase. Although many nonparasitic species are sympatric with their presumed parasitic ancestor, this is not always the case. For example, the nearest points in the distributions of the nonparasitic American Brook Lamprey (*Lethenteron appendix*) and its presumed ancestor, the Arctic Lamprey (*Lethenteron camtschaticum*), are >2,000 km apart (Vladykov & Kott 1978), which accounts for the highly disjunct distribution of *Lethenteron* (Fig. 3.3).

The Northern Hemisphere family Petromyzontidae contains 8 genera and 37 species (Table 3.1). In North America, this family is represented by 6 genera and 23 species of which 11 are parasitic and 12 are nonparasitic, the latter lifecycle category sometimes being referred to as brook Lampreys (Table 3.2). Four of the parasitic species undergo an anadromous migration, moving after metamorphosis from their larval habitats in fresh water to marine environments, where they feed parasitically before ultimately returning to rivers and streams to spawn. In contrast, the other seven parasitic species are confined to fresh water for the whole of their lifecycle (Table 3.1).

Petromyzontinae

Two of the Lamprey genera found in North America (*Petromyzon* and *Ichthyomyzon*) are members of one of two major clades within the Petromyzontidae, but four genera (*Tetrapleurodon*, *Entosphenus*, *Lethenteron*, and *Lampetra*) belong to the other major clade (see phylogenetic relationships section). The first clade constitutes the subfamily Petromyzontinae and the second the subfamily Lampetrinae (Table 3.1; Fig. 3.9). *Petromyzon marinus*, the sole representative of its genus, has an anadromous form that is widely distributed along the western and eastern seaboards of the North Atlantic Ocean, ranging in rivers in North America from Newfoundland in the north to Florida in the south (Fig. 3.4). Molecular studies strongly

Table 3.1. Classification, common names, lifecycles, and ranges of the species in the three extant families of Lampreys. In the lifecycle column, nonparasitic species are noted that can be unambiguously paired with a particular parasitic species. Asterisks denote species found in North America.

Classification	Common Name	Lifecycle	Range
Order Petromyzontiformes	Lampreys		
Family Mordaciidae	Southern Top-eyed Lampreys		
Genus *Mordacia*			
Mordacia mordax	Short-headed Lamprey	Anadromous, parasitic	Drainages of southeastern Australia
Mordacia praecox	Precocious Lamprey	Freshwater, nonparasitic derivative of *M. mordax*	Drainages of southeastern Australia
Mordacia lapicida	Chilean Lamprey	Anadromous, parasitic	Drainages of Chile
Family Geotriidae	Southern Striped Lamprey		
Genus *Geotria*			
Geotria australis	Pouched Lamprey	Anadromous, parasitic	Drainages of southern Australia, New Zealand, Chile, and Argentina
Family Petromyzontidae	Northern Hemisphere Lampreys		
Subfamily Petromyzontinae			
Genus *Caspiomyzon*			
Caspiomyzon wagneri	Caspian Lamprey	Anadromous, parasitic	Caspian Sea drainages
Genus *Petromyzon*			
*Petromyzon marinus**	Sea Lamprey	Anadromous and freshwater, parasitic	Drainages of North Atlantic, European Arctic, and Mediterranean Oceans/Seas
Genus *Ichthyomyzon*			
*Ichthyomyzon unicuspis**	Silver Lamprey	Freshwater, parasitic	Hudson Bay, Great Lakes, St. Lawrence River, and Mississippi River drainages
*Ichthyomyzon fossor**	Northern Brook Lamprey	Freshwater, nonparasitic derivative of *I. unicuspis*	As for *I. unicuspis*
*Ichthyomyzon castaneus**	Chestnut Lamprey	Freshwater, parasitic	Hudson Bay, Great Lakes, St. Lawrence River, and Gulf of Mexico drainages
*Ichthyomyzon gagei**	Southern Brook Lamprey	Freshwater, nonparasitic derivative of *I. castaneus*	Gulf of Mexico drainages
*Ichthyomyzon bdellium**	Ohio Lamprey	Freshwater, parasitic	Ohio River drainages
*Ichthyomyzon greeleyi**	Mountain Brook Lamprey	Freshwater, nonparasitic derivative of *I. bdellium*	As for *I. bdellium*
Subfamily Lampetrinae			
Genus *Tetrapleurodon*			
*Tetrapleurodon spadiceus**	Mexican Lamprey	Freshwater, parasitic	Celio, Duero, Zula, and Lerma Rivers, and Lake Chapala, Mexico
*Tetrapleurodon geminis**	Mexican Brook Lamprey	Freshwater, nonparasitic derivative of *T. spadiceus*	Celio and Duero Rivers, and Rio Grande de Morelia drainage, Mexico
Genus *Entosphenus*			
*Entosphenus tridentatus**	Pacific Lamprey	Anadromous and freshwater, parasitic	Drainages of western Canada, the United States, Mexico, and Japan

Table 3.1, continued

Classification	Common Name	Lifecycle	Range
*Entosphenus minimus**	Miller Lake Lamprey	Freshwater, parasitic	Upper Klamath River drainage, Oregon
*Entosphenus similis**	Klamath Lamprey	Freshwater, parasitic	Klamath River drainage, Oregon, and California
*Entosphenus macrostomus**	Vancouver Lamprey	Freshwater, parasitic	Lake Cowichan drainage, Vancouver Island, British Columbia
*Entosphenus folletti**	Northern California Brook Lamprey	Freshwater, nonparasitic	Klamath River drainage, California
*Entosphenus hubbsi**	Kern Brook Lamprey	Freshwater, nonparasitic	Friant-Kern Canal and Merced River, California
*Entosphenus lethophagus**	Pit-Klamath Brook Lamprey	Freshwater, nonparasitic	Klamath River drainage, Oregon, and Pit River, California
Genus *Lethenteron*			
*Lethenteron camtschaticum**	Arctic Lamprey	Anadromous and freshwater, parasitic	Drainages of Arctic and North Pacific Oceans
*Lethenteron alaskense**	Alaskan Brook Lamprey	Freshwater, nonparasitic derivative of *L. camtschaticum*	Drainages of Brooks and Chatanika Rivers, Alaska, and Mackenzie River, Canada
*Lethenteron appendix**	American Brook Lamprey	Freshwater, nonparasitic derivative of *L. camtschaticum*	Great Lakes drainages and eastern United States, St. Lawrence River, and Mississippi River drainages
Lethenteron reissneri	Far Eastern Brook Lamprey	Freshwater, nonparasitic derivative of *L. camtschaticum*	Drainages of Amur River, Sakhalin Island, and Kamchatka Peninsula, Russia, and in South Korea and Japan
Lethenteron kessleri	Siberian Brook Lamprey	Freshwater, nonparasitic derivative of *L. camtschaticum*	Drainages between Ob and Anadyr Rivers, and of Sakhalin Island, Russia, and Hokkaido Island, Japan
Lethenteron ninae	Western Transcaucasian Brook Lamprey	Freshwater, nonparasitic	Drainages of the Black Sea
Genus *Eudontomyzon*			
Eudontomyzon danfordi	Carpathian Lamprey	Freshwater, parasitic	Danube River drainage
Eudontomyzon mariae	Ukrainian Brook Lamprey	Freshwater, nonparasitic derivative of *E. danfordi*	Drainages of Baltic, Azov, Black, Adriatic, and Aegean Seas
Eudontomyzon stankokaramani	Drin Brook Lamprey	Freshwater, nonparasitic derivative of *E. danfordi*	Drainages of Adriatic Sea
Eudontomyzon morii	Korean Lamprey	Freshwater, parasitic	Yalu River drainage, China and North Korea
Eudontomyzon hellenicus	Macedonia Brook Lamprey	Freshwater, nonparasitic	Strymon River drainage, Greece
Eudontomyzon graecus	Epirus Brook Lamprey	Freshwater, nonparasitic	Loúros River drainage, Greece
Genus *Lampetra*			
*Lampetra ayresii**	Western River Lamprey	Anadromous and possibly freshwater, parasitic	Drainages of North American Pacific Coast
*Lampetra pacifica**	Pacific Brook Lamprey	Freshwater, nonparasitic derivative of *L. ayresii*	Drainages of Columbia River, Oregon, and Sacramento–San Joaquin Rivers, California

(continued)

Table 3.1, continued

Classification	Common Name	Lifecycle	Range
*Lampetra richardsoni**	Western Brook Lamprey	Freshwater, nonparasitic derivative of *L. ayresii*	Drainages of Pacific Ocean, British Columbia, Alaska, Washington, and Oregon
*Lampetra aepyptera**	Least Brook Lamprey	Freshwater, nonparasitic	Drainages of northwestern Atlantic Ocean and Gulf of Mexico, United States
Lampetra fluviatilis	European River Lamprey	Anadromous and freshwater, parasitic	Drainages of northeastern Atlantic Ocean
Lampetra planeri	European Brook Lamprey	Freshwater, nonparasitic derivative of *L. fluviatilis*	As for *L. fluviatilis*, plus Danube and Volga River drainages
Lampetra zanandreai	Po Brook Lamprey	Freshwater, nonparasitic	Drainages of Adriatic Sea
Lampetra lanceolata	Turkish Brook Lamprey	Freshwater, nonparasitic derivative of *L. fluviatilis*	Iyidere River, Turkey

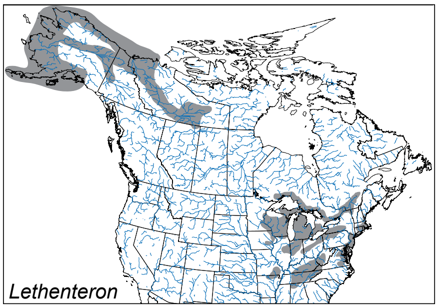

Figure 3.3. Geographic range of *Lethenteron* in North America.

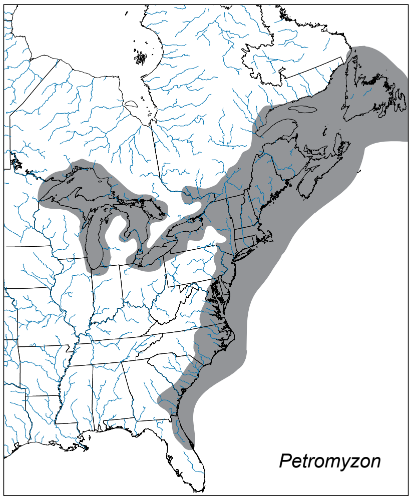

Figure 3.4. Geographic range of *Petromyzon* in North America.

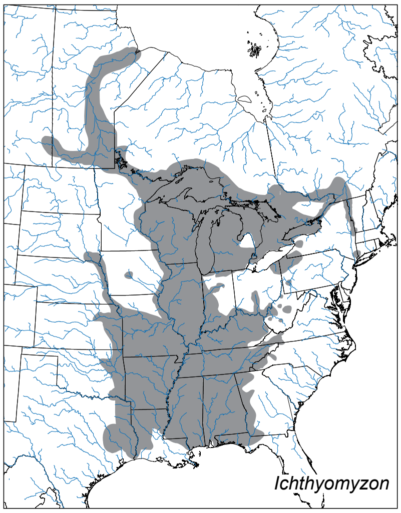

Figure 3.5. Geographic range of *Ichthyomyzon*.

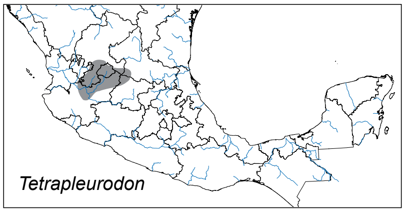

Figure 3.6. Geographic range of *Tetrapleurodon*.

indicate that the populations of the anadromous Sea Lampreys on either side of the Atlantic Ocean do not mix (Rodríguez-Muñoz et al. 2004). The landlocked derivative of the anadromous *P. marinus*, which is likewise parasitic, is abundant in Lakes Oneida and Cayuga and the Laurentian Great Lakes and their tributaries. The genus *Ichthyomyzon* is confined to the fresh waters of eastern North America (Table 3.1; Fig. 3.5) that are tributary to the Gulf of Mexico, St. Lawrence River, and Hudson Bay (Hubbs & Trautman 1937; Hubbs & Potter 1971). This genus contains three parasitic species, the Silver Lamprey (*Ichthyomyzon unicuspis*), Chestnut Lamprey (*Ichthyomyzon castaneus*), and Ohio Lamprey (*Ichthyomyzon bdellium*), and their respective derived nonparasitic species,

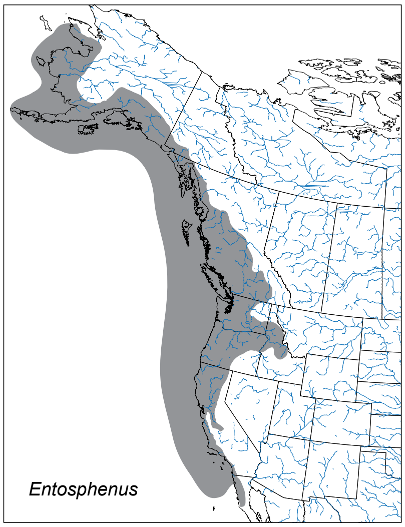

Figure 3.7. Geographic range of *Entosphenus* in North America.

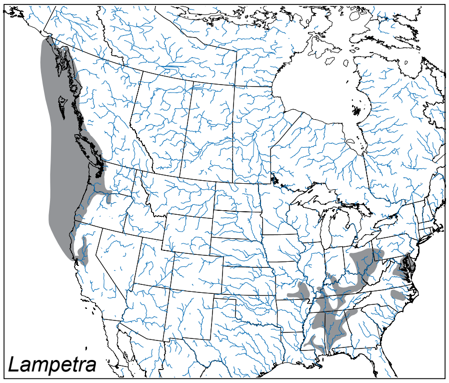

Figure 3.8. Geographic range of *Lampetra* in North America.

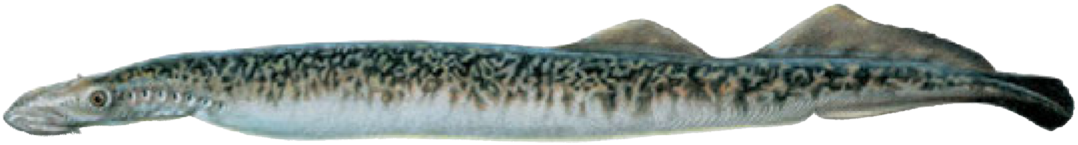

Plate 3.1. Sea Lamprey, *Petromyzon marinus*

the Northern Brook Lamprey (*Ichthyomyzon fossor*), Southern Brook Lamprey (*Ichthyomyzon gagei*), and Mountain Brook Lamprey (*Ichthyomyzon greeleyi*, formerly *I. hubbsi*) (Table 3.1).

Lampetrinae

Among the four genera found in North America that belong to the second clade of petromyzontids, the genus *Tetrapleurodon* is endemic to the fresh waters of the Mexican Plateau (Fig. 3.6) and contains one parasitic species, the Mexican Lamprey (*Tetrapleurodon spadiceus*), and its nonparasitic derivative, the Mexican Brook Lamprey (*Tetrapleurodon geminis*) (Table 3.1). The genus *Entosphenus* comprises seven species that includes the Pacific Lamprey (*Entosphenus tridentatus*), a large and anadromous parasitic species, whose distribution in fresh water extends widely in a broad arc along the eastern seaboard of the Pacific Ocean from the northern part of Mexico in the south to Alaska in the north (Fig. 3.7) and then into northern Japan in the Western Pacific Ocean (Potter & Gill 2003). Three other species of *Entosphenus*, the Miller Lake Lamprey (*Entosphenus minimus*), Klamath Lamprey (*Entosphenus similis*), and Vancouver Lamprey (*Entosphenus macrostomus*), are also parasitic but are far smaller than *E. tridentatus* and confined for their entire lifecycle to single drainages of the Pacific Ocean. The three nonparasitic species of *Entosphenus*, the Northern California Brook Lamprey (*Entosphenus folletti*), Kern Brook Lamprey (*Entosphenus hubbsi*), and Pit-Klamath Brook Lamprey (*Entosphenus lethophagus*), occur in drainages within a restricted area in the southern part of the range of *E. tridentatus* (Table 3.1).

Three of the seven species of *Lethenteron* are found in North America (Potter & Gill 2003; Fig. 3.3). These include the parasitic species, the Arctic Lamprey (*Lethenteron camtschaticum*), which occurs in drainages of the Arctic and North Pacific Oceans and contains both anadromous and freshwater forms. The Alaskan Brook Lamprey (*Lethenteron alaskense*), one of the nonparasitic derivatives of *L. camtschaticum*, is restricted to rivers in Alaska and northwestern Canada, and the other nonparasitic species, *L. appendix*, occurs only in drainages of the eastern seaboard of North America and the Gulf of Mexico (Fig. 3.3).

The seven species of *Lampetra* contain four that are endemic to North America, two that are endemic to Europe, and one that is endemic to Asia. In North America, this genus has a disjunct distribution similar to that of *Lethenteron* (Fig. 3.8). The anadromous parasitic Western River Lamprey (*Lampetra ayresii*) is found in the drainages of the North American Pacific Coast, encompassing those in

Table 3.2. Lifecycle characteristics of Lampreys found in North America. Length and weight are for adults.

General Characteristics	Characteristics of Lifecycle Categories
Total number of species 23 *Lifecycle mode* Anadromous and parasitic, freshwater and parasitic, or freshwater and nonparasitic *Spawning* Semelparous Duration: May to August (except *Tetrapleurodon* spp.—November to January) Habitat: shallows of rivers, streams, or lakes Eggs: about 1 mm in diameter, buried in gravel or sand, in shallow water (typically <1 m) Hatching time: 10–13 days at 18°C Larval type: proto-larva Mean length at hatching: 3–5 mm Male is major nest builder *Larva (ammocoete)* Habitat: burrows in soft substrates of slow-flowing areas of rivers and streams Diet: detritus, bacterial mats, diatoms, and other microorganisms *Adult* Habitat Parasitic species: seas, lakes, and rivers Nonparasitic species: small rivers and streams Diet Parasitic species: blood or muscle of fish Nonparasitic species: do not feed as adults *Imperilment status* Many populations and a few species are imperiled	*Anadromous and parasitic* 4 species Length (mm TL): 110–1,200 Weight (g): 2–2,300 Lifecycle duration: several years Fecundity: 10,000–305,000 Migration: downstream movement (after metamorphosis) to the sea and an upstream migration of adults to their spawning areas. All four species have derivative and permanent freshwater, parasitic populations *Exclusively freshwater and parasitic* 7 species Length (mm TL): 70–390 Weight (g): 2–75 Lifecycle duration: several years Fecundity. 500–29,000 Migration: downstream movement (after metamorphosis) to lakes and larger areas of rivers for feeding and an upstream migration by adults to their spawning areas *Freshwater and nonparasitic* 12 species Length (mm TL): 80–220 (exceptionally 320) Weight (g): 2–8 (exceptionally 80) Lifecycle duration: several years Fecundity: 600–4,600 Migration: upstream movement by adults to their spawning areas

which its nonparasitic derivative *L. richardsoni* is found. The latter species is considered also to be represented by a freshwater trophic form that has been termed *L. richardsoni* var. *marifuga* (Beamish & Withler 1986; Youson & Beamish 1991; Youson 2004), but we consider it to be a freshwater resident form of *L. ayresii* (Table 3.1). The distribution of *L. ayresii* also encompasses the more restricted range of another nonparasitic species, the Pacific Brook Lamprey (*Lampetra pacifica*). The Least Brook Lamprey (*Lampetra aepyptera*) occurs in drainages of the Atlantic Ocean and Gulf of Mexico (Table 3.1; Fig. 3.8). Whether this species should be assigned to *Lampetra* or to its own genus *Okkelbergia* has been debated (see Hubbs & Potter 1971; Vladykov & Kott 1976; Docker et al. 1999; Lang et al. 2009). This controversy is due to this species having a highly degenerate and reduced dentition (Fig. 3.10), and thus not possessing the most informative of the morphological characters that are used for assigning Lampreys at the generic level (Gill et al. 2003). Nevertheless, the results of molecular studies provide good evidence that the parasitic species that are most closely related to this nonparasitic Lamprey are members of the genus *Lampetra*. Here, we follow Docker (2009) in retaining this species in *Lampetra*, while recognizing that further molecular studies are required to validate this decision.

Distribution and Body Size

Comparisons of the distributions of Lamprey species show that the species with the widest distributions are those with a marine trophic phase and that attain the largest body sizes (e.g., *P. marinus* and *E. tridentatus* in the Northern Hemisphere, and *G. australis* in the Southern Hemisphere; Hubbs & Potter 1971). In this regard, tagging and molecular studies provide strong evidence that at least the landlocked and anadromous forms of the Sea Lamprey do not home to their natal rivers (Bergstedt & Seelye 1995; Rodríguez-Muñoz et al. 2004; Waldman et al. 2008a) and

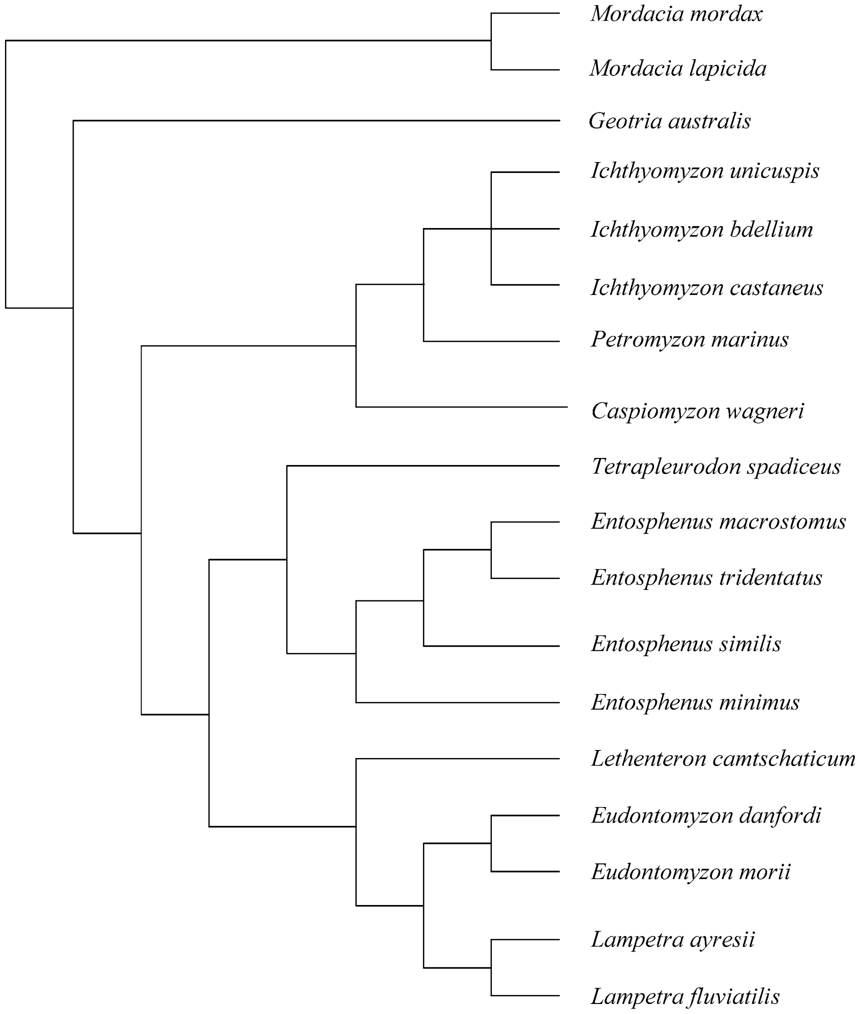
Mordacia mordax
Mordacia lapicida
Geotria australis
Ichthyomyzon unicuspis
Ichthyomyzon bdellium
Ichthyomyzon castaneus
Petromyzon marinus
Caspiomyzon wagneri
Tetrapleurodon spadiceus
Entosphenus macrostomus
Entosphenus tridentatus
Entosphenus similis
Entosphenus minimus
Lethenteron camtschaticum
Eudontomyzon danfordi
Eudontomyzon morii
Lampetra ayresii
Lampetra fluviatilis

Figure 3.9. Phylogenetic relationships among the parasitic species of the three families of Lampreys, derived from a combination of separate cladistic analyses of morphological and molecular (mitochondrial cytochrome *b*) data.

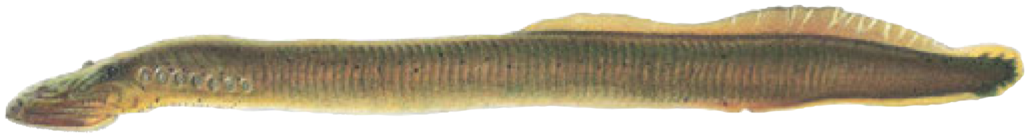

Plate 3.2. Chestnut Lamprey, *Ichthyomyzon castaneus*

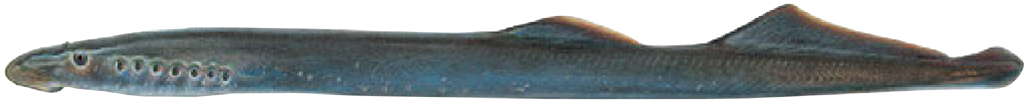

Plate 3.3. Pacific Lamprey, *Entosphenus tridentatus*

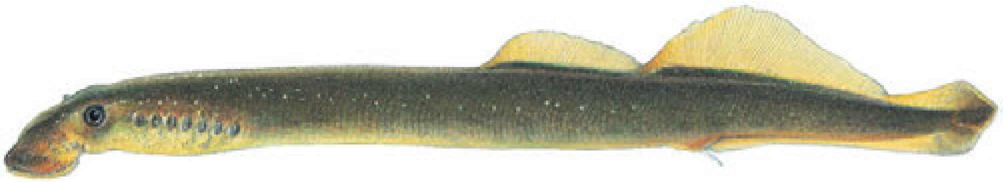

Plate 3.4. American Brook Lamprey, *Lethenteron appendix*

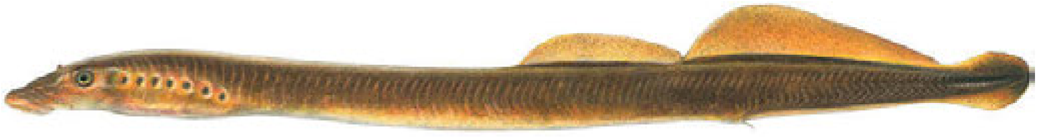

Plate 3.5. Western Brook Lamprey, *Lampetra richardsoni*

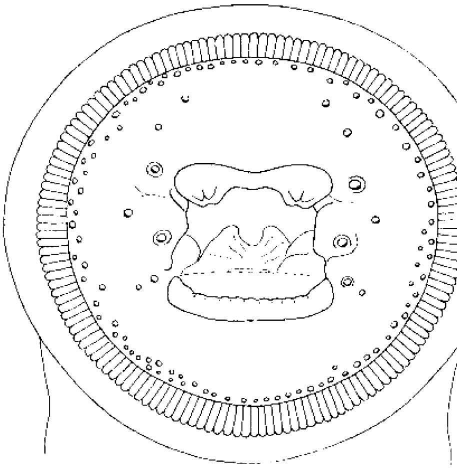

Figure 3.10. Oral disc of the Least Brook Lamprey, *Lampetra aepyptera*, showing the highly degenerate dentition of this nonparasitic species (reprinted from *The Biology of Lampreys*, Vol 1, M. W. Hardisty and I. C. Potter, eds., C. L. Hubbs and I. C. Potter, Distribution, Phylogeny and Taxonomy, pages 1–65, 1971).

thus have the potential to colonize new areas. Indeed, *P. marinus*, *E. tridentatus*, and *G. australis* range widely in the marine environment (Potter et al. 1979; Halliday 1991; Renaud 2008). The smaller anadromous species, such as *L. ayresii* in North America and its analogue, the European River Lamprey (*Lampetra fluviatilis*), in Europe, have a more coastal distribution, and although also distributed widely, their ranges are not as great as those of *P. marinus*, *E. tridentatus*, and *G. australis*. In contrast, freshwater parasitic species, such as *T. spadiceus* and the three species of *Ichthyomyzon*, are each confined to one or a few large drainages, which in the case of *Ichthyomyzon* spp., penetrate deeply into the North American continent (Table 3.1). Although the distribution of a nonparasitic species sometimes largely mirrors that of its parasitic ancestor (e.g., the nonparasitic European Brook Lamprey, *Lampetra planeri*, and the parasitic *L. fluviatilis* in Europe), the nonparasitic species sometimes occupy only a small part of the range of the parasitic ancestor (e.g., the nonparasitic species derived from *E. tridentatus*), or differ markedly, as with the nonparasitic *L. appendix* and the parasitic *L. camtschaticum* (see previous section).

PHYLOGENETIC RELATIONSHIPS

Family and Generic Relationships

A cladistic analysis of a range of morphological and other phenotypic characters of 18 species of parasitic Lampreys yielded the following 4 synapomorphies (shared, derived characters) for adults that support the monophyly of the extant Lampreys (Gill et al. 2003): alate rows of teeth in the anterior field or all fields of the oral disc (Fig. 3.2); an infraoral lamina (Fig. 3.2); a diphycercal caudal fin (Fig. 3.1); and an otic capsule located directly above or slightly anterior to the first branchial opening. Four synapomorphies for adults supported the monophyly of the Petromyzontidae: three or four lateral circumoral teeth on each side of the oral aperture; the continuity or contiguousness of the two dorsal fins in mature adults; a gular pouch that is either small or absent in mature males; and the location of the cloaca under the anterior half of the second dorsal fin in mature adults.

Although the use of phenotypic characters did not resolve the interrelationships of the three families (Gill et al. 2003), a recent Bayesian analysis, using data for cytochrome *b* for almost all known parasitic and nonparasitic species, provided strong evidence that the Geotriidae are sister to the Petromyzontidae (Lang et al. 2009). Although the cladograms derived from the phenotypic and molecular data sets for parasitic species are generally in good agreement, they differ in the following four respects.

First, in contrast to the phylogenetic tree derived from phenotypic data in which the genera *Petromyzon* and *Ichthyomyzon* form a clade that is sister to all other Northern Hemisphere Lamprey genera, the Bayesian analysis of cytochrome *b* data included the genus *Caspiomyzon* in the *Petromyzon* + *Ichthyomyzon* clade (Lang et al. 2009; and our unpublished reanalysis of their data using as outgroups two subfamilies of Hagfishes rather than the cephalochordate *Branchiostoma*). The conclusion that the genus *Caspiomyzon* is closely related to *Petromyzon* is supported by the strong posterior probabilities in the Bayesian analyses using molecular data. It is also consistent with the proposal that the sole species of *Caspiomyzon*, the Caspian Lamprey (*Caspiomyzon wagneri*), evolved from a form similar to *P. marinus* that became isolated in the Caspian Sea (Hubbs & Potter 1971). The second difference was recognition of a *Tetrapleurodon* + *Entosphenus* clade rather than an *Entosphenus*, *Lethenteron*, *Eudontomyzon* + *Lampetra* clade, a scenario consistent with the earlier scheme of Vladykov & Kott (1979a). The third difference between the results of phenotypic and molecular analyses resided in the *Lampetra* species from North America and Europe forming a strongly supported monophyletic group only when using morphological data. The fourth difference is that, in contrast to the morphological analyses, the molecular analyses indicated that the Mordaciidae were paraphyletic. This was surprising given that there were 10 phenotypic synapomorphies supporting the monophyly of the two parasitic species of Mordaciidae (Gill et al. 2003). Further, in our reanalysis of the data of Lang et al. (2009), the monophyly of the Mordaciidae had a Bayesian posterior probability of 1.0. For these reasons, the proposed hypotheses regarding relationships among the parasitic species of Lampreys (Fig. 3.9) is the same as that of Gill et al. (2003), except that *C. wagneri* is sister to *Petromyzon* + *Ichthyomyzon*; *Tetrapleurodon* is sister to *Entosphenus*; and the Mordaciidae are sister to the Geotriidae + Petromyzontidae.

Analysis of cDNA data suggested that Northern Hemisphere Lampreys and the Geotriidae diverged between 280 and 220 mya, and those for cytochrome *b* and ND3 mitochondrial genes indicated that, within the Petromyzontidae, the genus *Petromyzon* diverged from *Lampetra* and *Lethenteron* between 30 and 10 mya (Docker et al. 1999; Kuraku & Kuratani 2006).

Characteristics and Evolution of Nonparasitic Species

The majority of nonparasitic species can be paired unambiguously with a particular parasitic species on the basis of the close similarity in one or more of the following: their morphology, and particularly the types and arrangement of their dentition (e.g., Hubbs & Trautman 1937; Potter et al. 1968a; Hardisty et al. 1970; Hubbs & Potter 1971; Vladykov & Kott 1979b); the composition of the base pairs of mitochondrial cytochrome *b* and ND3 (Docker 2009; Lang et al. 2009); and allozyme data (Yamazaki & Goto 1998). Such clear pairing of nonparasitic species with parasitic species in North America is exhibited by the pairing of each of the three nonparasitic species of *Ichthyomyzon* with their corresponding parasitic ancestors; *L. richardsoni* and *L. pacifica* with *L. ayresii*; *T. geminis* with *T. spadiceus*; and *L. alaskense* and *L. appendix* with *L. camtschaticum* (Table 3.1). The corresponding pairs elsewhere in the Northern Hemisphere are *L. planeri* with *L. fluviatilis*; the Ukrainian Brook Lamprey (*Eudontomyzon mariae*) and *E. stankokaramani* with the Carpathian Lamprey (*Eudontomyzon danfordi*); and the Far Eastern Brook Lamprey (*Lethenteron reissneri*) and Siberian Brook Lamprey (*Lethenteron kessleri*) with *L. camtschaticum*. The Precocious Lamprey (*Mordacia praecox*) and the Short-headed Lamprey (*Mordacia mordax*) constitute the only paired species in the Southern Hemisphere.

In contrast to the above 14 nonparasitic species, which each have a dentitional arrangement similar to that of a particular parasitic species, the dentition of *L. aepyptera* is highly degenerate and contains only a few small, blunt teeth (Fig. 3.10). This led to the hypothesis that, relative to the other 14 nonparasitic species, *L. aepyptera* has been separated from its parasitic ancestor for a much longer period (Docker 2009). Indeed, there is no obvious candidate for the ancestor of this species. Further, *Lampetra*, the genus to which this species has often been allocated, is not represented by a parasitic species in drainages of the Gulf of Mexico or the eastern seaboard of North America where *L. aepyptera* occurs. Molecular data suggest that its closest parasitic relative among *Lampetra* species is *L. fluviatilis*, which is confined to European waters (Docker et al. 1999). If the implications of the molecular data are correct, *L. fluviatilis*, or an ancient ancestor of that species, may have given rise to *L. aepyptera* in North America and then became extinct in that continent. Further molecular studies are clearly needed to provide a wider range of genes from both the mitochondrial and nuclear genomes to explore the relationships of *L. aepyptera* in a zoogeographical context.

On the basis of the results of a molecular study, a number of nonparasitic species appeared to belong to a different genus than that to which they had been assigned using morphological criteria (Lang et al. 2009). Thus, for example, recent molecular studies suggest that the Po Brook Lamprey (previously *Lethenteron zanandreai*) is closely related to the nonparasitic Turkish Brook Lamprey (*Lampetra lanceolata*) and is more closely related to *L. fluviatilis* than to any *Lethenteron* species (Lang et al. 2009), which is consistent with Vladykov & Kott (1979b). The species *zanandreai* is therefore now assigned to *Lampetra* (Table 3.1). Molecular studies also indicated that the Macedonia Brook Lamprey (*Eudontomyzon hellenicus*) is closely related to *C. wagneri* and that the Kern Brook Lamprey (*Entosphenus hubbsi*) is more closely related to *L. ayresii* than to any species of *Entosphenus*. If confirmed in the future, the above relationships would necessitate a change in the generic status of those two nonparasitic species. It is unclear whether the nonparasitic Pit-Klamath Brook Lamprey (*Entosphenus lethophagus*) and the Northern California Brook Lamprey (*Entosphenus folletti*) are derived from the anadromous parasitic *E. tridentatus* or the freshwater parasitic *E. similis* with which they are sympatric. The nonparasitic Western Transcaucasian Brook Lamprey (*Lethenteron ninae*) and the Epirus Brook Lamprey (*Eudontomyzon graecus*) have yet to be included in a molecular study. The above comparisons highlight the need to resolve, at the generic level, anomalies between the results of analyses for nonparasitic species using morphological and molecular data by employing a wider range of genes from both the mitochondrial and nuclear genomes.

Detailed comparisons of aspects of the biology of the nonparasitic *L. planeri* and those of its presumed ancestor the anadromous parasitic *L. fluviatilis* in Europe have elucidated some of the changes that presumably took place during the evolution of that nonparasitic species and of such species in general (Hardisty & Potter 1971c). These comparisons strongly indicate that, on average, *L. planeri* has a longer larval life than *L. fluviatilis* (i.e., 6.25 versus 4.25 years, respectively) (Fig. 3.11), and thus typically metamorphoses at a larger size. Gonadal maturation in *L. planeri* commences during metamorphosis, and this leads to sexual maturation and spawning occurring in the natal stream after only about 9 months since the end of larval life (i.e., after a total life span of 7 years). In contrast, the completion of metamorphosis after a few months in *L. fluviatilis* is followed by a downstream migration to the sea, where this species feeds parasitically and grows rapidly for about 18 months. At the completion of this marine trophic phase, *L. fluviatilis* re-enters rivers where it spends about 9 months migrating upstream and attaining maturity and spawning. Thus, like the nonparasitic *L. planeri*, *L. fluviatilis* breeds at the end of its seventh year of life and therefore, on average, has the same lifespan as its nonparasitic derivative (Fig. 3.11).

From the above interspecific differences, it follows that the evolution of the nonparasitic *L. planeri* from the parasitic *L. fluviatilis* has involved a change in the timing of the various phases in the lifecycle, rather than an acceleration in the timing of sexual maturation. As a consequence of the elimination of the adult trophic phase, the size of the fully mature adult of *L. planeri* is far smaller than that of *L. fluviatilis* (Hardisty & Potter 1971c). As the larvae of other nonparasitic species also typically attain larger body sizes than those of their presumed parasitic ancestors, the same changes have probably occurred during the evolution of all nonparasitic species. Indeed, there is even evidence that the evolution of the landlocked parasitic populations of *P. marinus* from the anadromous populations of this species involved an increase in the duration of larval life and a corresponding reduction in the duration of the parasitic phase and thus, likewise, no change in the overall length of life (Lowe et al. 1973; Potter & Beamish 1977; Potter 1980a).

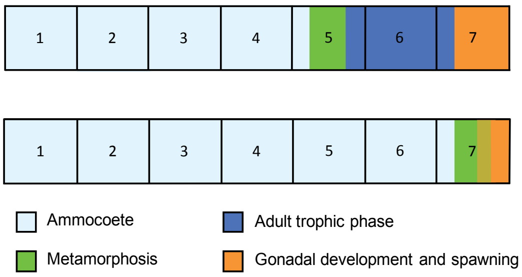

Figure 3.11. A comparison of the durations of the different phases in the lifecycles of the anadromous and parasitic European River Lamprey, *Lampetra fluviatilis* (*top*) and its nonparasitic derivative, the European Brook Lamprey, *Lampetra planeri* (*bottom*).

During the evolution of the nonparasitic *L. planeri* from the parasitic *L. fluviatilis*, gonadogenesis commenced earlier in larval life (Hardisty 1971). While this was accompanied by a reduction in the potential fecundity (total number of oocytes) of ammocoetes of the nonparasitic species by a factor of about 2.5 times, the absolute fecundity of adult *L. planeri* is only about one-tenth of that of adult *L. fluviatilis*. Yet, the diameters of the oocytes of *L. planeri* and *L. fluviatilis* are similar at the commencement of metamorphosis (i.e., about 0.1 mm) and at maturity (about 1 mm). Thus, because the body size and therefore ovarian volume of adult *L. planeri* at maturity are far less than those of adult *L. fluviatilis* in the same geographical region (Hardisty 1961; Abou-Seedo & Potter 1979), the oocyte complement in *L. planeri* must undergo a massive reduction in number prior to the attainment of maturity. This is achieved through extensive atresia during metamorphosis.

As with the above paired species of *Lampetra*, the potential fecundity of the ammocoetes of the nonparasitic *I. gagei* is less than that of its parasitic ancestor *I. castaneus* (Beamish & Thomas 1983), and the same is true for the species pair comprising the nonparasitic *M. praecox* and the anadromous parasitic *M. mordax* (Hughes & Potter 1969). During the metamorphosis of *M. praecox* and *L. reissneri*, their oocytes undergo extensive atresia and consequently the absolute fecundities of the mature adults of these two nonparasitic species are far less than the potential fecundities of their ammocoetes (Hughes & Potter 1969; Fukayama & Takahashi 1983). In contrast, the absolute fecundities of the nonparasitic species *I. gagei* and *L. aepyptera* do not differ significantly from their potential fecundities (Beamish & Thomas 1983; Docker & Beamish 1991). The lack of such a difference in *L. aepyptera* presumably reflects the long period that this nonparasitic species is believed to have been separated from its parasitic ancestor and that would thereby have provided sufficient time for natural selection to have led to a balance between potential and absolute fecundity.

The above comparisons elucidate how the two main phenotypic differences between each nonparasitic species and its parasitic ancestor (i.e., far smaller body size and absolute fecundity of adults) were derived through alterations in the timing of reproductive and somatic development (i.e., by heterochrony). Since optimal spawning behavior by Lampreys involves the male coiling around and squeezing the eggs out of a similar-sized female, the large differences in the body size of a nonparasitic species and its parasitic ancestor act as a deterrent to interbreeding between the members of paired species (Hardisty & Potter 1971c; Beamish & Neville 1992; Docker 2009). Further, the strong tendency for nonparasitic species to spawn in areas that are shallower and slower flowing and that contain smaller gravel than areas where parasitic species breed also helps act as an isolating mechanism between the members of species pairs (Hardisty & Potter 1971c; Docker 2009).

The presence of certain nonparasitic species, such as *L. richardsoni*, in numerous river systems and the confinement of each population of such species to its natal stream implies that each of these populations arose as an independent lineage. Although each population of a particular nonparasite is therefore not technically a true species, most Lamprey taxonomists recognize lifecycle type (i.e., parasitic versus nonparasitic) as a species-specific characteristic and thus regard the different populations of a given nonparasitic morphotype as a species (Docker 2009).

Genetic differences between sympatric populations of paired nonparasitic and parasitic species are known thus far only in those comprising the nonparasitic species *L. reissneri* and *L. kessleri* and their common parasitic ancestor *L. camtschaticum* (Yamazaki & Goto 1998). In the case of allopatric species, genetic differences exist between the nonparasitic *L. appendix* and parasitic *L. camtschaticum* (Docker et al. 1999), which are separated geographically by >2,000 km (see diversity and distribution section).

The question of which selection pressures may have led to the evolution of nonparasitic species has been addressed in several reviews (e.g., Salewski 2003; Hardisty 2006; Docker 2009). Nonparasitic species possibly arose when barriers brought about by advances and retreats of glaciers 10,000–15,000 years ago prevented the migration of parasitic species from and into river systems (Docker 2009). This relatively recent time period could account for those paired species in which the dentitional characters of the nonparasitic and parasitic species are particularly similar. A decline in the abundance of suitable hosts may also have been a factor in the selection for a nonparasitic mode of life. Assuming near equal rates of evolutionary change, variation in the extent of degeneration in the dentition of nonparasitic species indicates that nonparasitic species have evolved at different times. Indeed, Docker (2009) proposed that the extent of differences between the members of species pairs reflects the following five sequential stages in the speciation of nonparasitic Lampreys:

1. Parasitic species with no nonparasitic counterparts
2. Polymorphic population producing both parasitic and nonparasitic forms
3. Paired species without fixed morphological or genetic differences
4. Paired species with fixed genetic differences
5. Nonparasitic species that have been isolated for a long period from their parasitic ancestor, which may no longer be represented in the contemporary fauna

Docker has also recognized that some typically anadromous parasitic species are represented in fresh water by parasitic praecox (premature) forms that are far smaller than the anadromous form and thus presumably have a shorter adult trophic phase and that in the past may have constituted an important intermediate stage in the evolution of certain nonparasitic species. Hardisty (2006) and Docker (2009) present excellent reviews and more detailed discussions of the ways that nonparasitic species may have evolved.

FOSSIL RECORD

The first recorded fossil Lamprey, †*Mayomyzon pieckoensis* (Fig. 3.12), was described from the Upper Carboniferous (about 280 mya) deposits of Mazon Creek, Illinois (Bardack & Zangerl 1971). The excellently preserved fossils possessed an annular cartilage in the same position as in extant Lampreys, where it plays a crucial role in maintaining the structural integrity of the suctorial disc of adults (Lanzing 1958). †*Mayomyzon pieckoensis* also possessed well-developed eyes, which in living Lampreys develop after the completion of metamorphosis. Although this fossil Lamprey possessed these important adult characteristics, its largest specimen was only 60 mm TL, which is less than the minimum length at which any extant parasitic species enters metamorphosis. Further, †*M. pieckoensis* possessed a relatively smaller oral disc than contemporary Lampreys

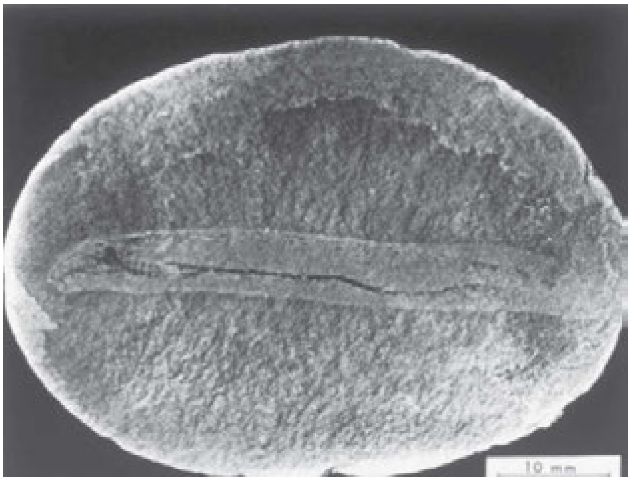

Figure 3.12. †*Mayomyzon pieckoensis*, the first fossil Lamprey to be described (reprinted from *The Biology of Lampreys*, Vol 1, M. W. Hardisty and I. C. Potter, eds., D. Bardack and R. Zangerl, Lampreys in the Fossil Record, pages 67–84, 1971).

and did not contain the teeth that are so distinctive of the adults of living Lampreys. These features suggest that †*M. pieckoensis* was a scavenger rather than a parasite (Hardisty 1979).

The fossil Lamprey †*Hardistiella montanensis* (from about 325 mya) was found in Carboniferous deposits in North America, as was †*Pipiscius zangerli* (from about 310 mya), which is possibly a Lamprey (Bardack & Richardson 1977; Janvier & Lund 1983; Janvier et al. 2004). The fossils of †*H. montanensis* contained a structure that could have been a complex sucking device, but the fossils showed no evidence of having piston, tectal, or annular cartilages. The disc of †*P. zangerli* bears a ring of simple tooth plates around the oral aperture. Like the fossils of †*M. pieckoensis*, those of †*H. montanensis* are small (i.e., <100 mm TL).

The discovery of a beautifully preserved fossil of a single †*Priscomyzon riniensis* in South Africa (Gess et al. 2006) shows that Lampreys with dentition inhabited marine or estuarine waters during the Devonian (about 360 mya), and two equally well-preserved fossils of †*Mesomyzon mengae* in China (Fig. 3.13; Chang et al. 2006) demonstrate that Lampreys were present in fresh waters during the Cretaceous (about 125 mya). Notably, †*M. mengae* has an otic capsule located just anterior to the first branchial pouch and a diphycercal tail, which are both synapomorphies of the extant Lampreys (Gill et al. 2003). Like the North American fossils, the South African and Chinese fossil Lampreys are all <100 mm TL.

Based on a single poorly preserved specimen of †*Haikouichthys ercaicunensis*, Shu et al. (1999) suggested that the petromyzontiform lineage extended to the Lower Cambrian (about 520 mya). Analyses of more recent discoveries of >500 fossils of †*H. ercaicunensis* indicate, however, that this species is a stem-group craniate and not a Lamprey (Shu et al. 2003).

MORPHOLOGY

Although the larvae of Lampreys undergo a radical metamorphosis into adults, these divergent lifecycle stages share some important morphological characteristics. Thus, the ammocoete and adult are both eel-shaped, and possess seven pairs of gills with external openings, dorsal fins that are continuous with the caudal fin, a single blind median nostril, and two semicircular canals, and neither has scales or bones, or pectoral, pelvic, or anal fins (Fig. 3.1; Hardisty 1982).

Most of the morphological differences between ammocoetes and adults represent adaptations for a relatively sedentary burrowed life versus a more active mode of life and for a microphagous rather than parasitic mode of feeding. The ammocoetes of all Lamprey species are morphologically similar and adapted for living in burrows in the soft substrates of streams and rivers and obtaining food from the overlying water (Hardisty & Potter 1971ab; Moore & Mallatt 1980). In contrast, the adults of parasitic species are adapted for both free swimming and attachment to predominantly actinopterygian fishes from which they extract their food (Hardisty & Potter 1971b; Renaud et al. 2009a). Thus, e.g., in comparison with ammocoetes, adult Lampreys have far larger fins and well-developed rather than rudimentary eyes (Kleerekoper 1972; Collin 2007).

Size

In North America and elsewhere, Lampreys typically complete their larval life and enter metamorphosis at 80–160 mm TL. The size varies among species and even populations of the same species (e.g., Potter 1970; Hardisty & Potter 1971c; Potter & Bailey 1972; Beamish & Potter 1975; Potter & Hilliard 1986; Medland & Beamish 1987) and between males and females (e.g., Medland & Beamish 1987; Docker & Beamish 1994). The lengths attained during the parasitic phase vary greatly among species and between those that are parasitic in marine and freshwater environments (Hardisty & Potter 1971b). Thus, among anadromous parasitic species, *P. marinus* and *E. tridentatus* can attain >750 mm TL, but *L. ayresii* rarely is

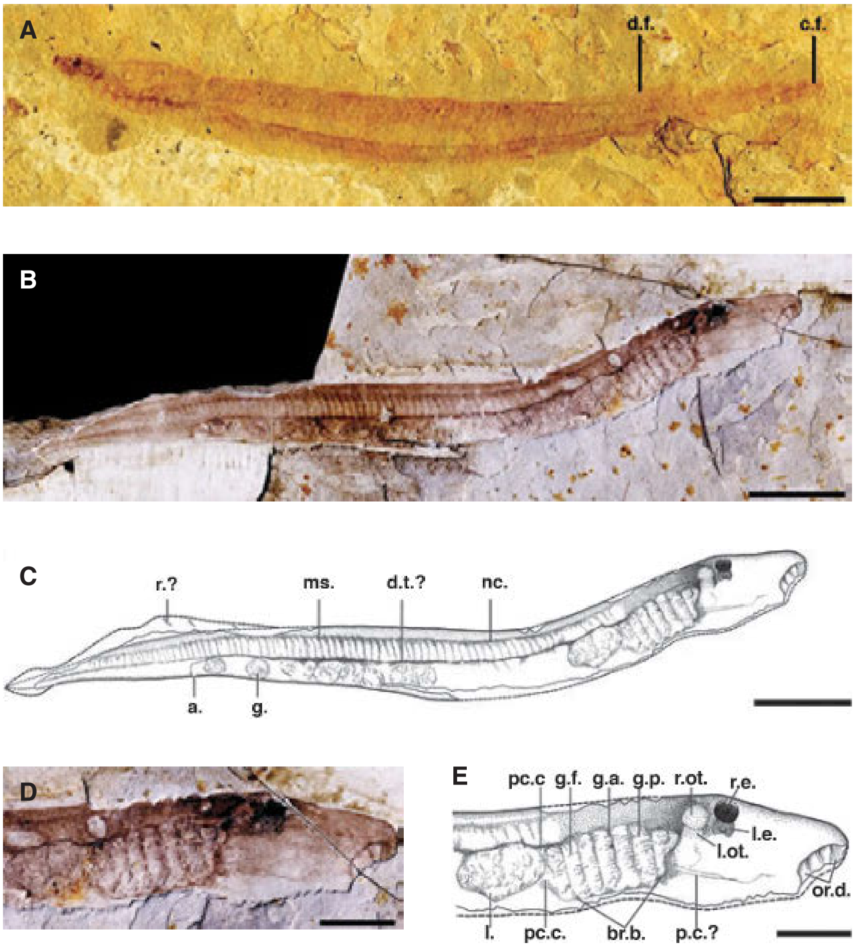

Figure 3.13. †*Mesomyzon mengae*, the youngest fossil Lamprey to be described: (A) a complete fossil in left view, (B) holotype in right view, (C) reconstruction of holotype, (D) head and anterior part of body, (E) reconstruction of d. Scale bars (A–C) 10 mm, (D, E) 5 mm. Abbreviations: a, anus; br.b., branchial basket; c.f., caudal fin; d.f., dorsal fin; d.t.?, possible digestive tract; g., gonads; g.a., gill arches; g.f., gill filaments; l., liver; l.e., left eye; l.ot., left otic capsule; ms., myosepta; nc., notochord; or.d., oral disc; p.c.?, possible piston cartilage; pc.c., pericardial cartilage; r.e., right eye; r.ot., right otic capsule (reprinted by permission from Macmillan Publishers Ltd: Nature, Chang et al. 2006).

>300 mm TL, and among freshwater species those of *Ichthyomyzon* typically reach 200–300 mm TL, and the maximum size of *E. minimus* is 150 mm TL. Because each nonparasitic species does not feed after completing its larval phase and undergoes some shrinkage during sexual maturation, the maximum length of its adult is slightly less than that of its ammocoete.

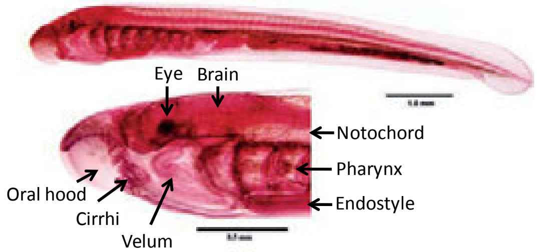

Figure 3.14. Cleared and stained larval Lamprey (ammocoete): whole animal (*top*) and anterior region (*bottom*).

Feeding Mechanisms of Ammocoetes

The ability of ammocoetes to ingest detritus, bacteria, diatoms, and other microorganisms is facilitated by their possession of a large oral hood that helps direct food toward the pharynx (Fig. 3.14). A ring of oral cirrhi at the entrance of the pharynx acts as a sieve, preventing large particles from passing into the branchial chamber. The muscular actions of the velum and branchial chamber move food and water into the pharynx, where the food is trapped on mucous strands and exposed to digestive enzymes produced by the prominent endostyle that is located at the base of the pharyngeal chamber (Moore & Mallatt 1980; Youson 1981). The food is then passed backward into the simple intestine where further digestion and then assimilation occur (Cake et al. 1992). The water drawn into the pharynx is passed out over the well-developed gills, which have a large surface area that facilitates the extraction of the oxygen required for metabolism (Lewis & Potter 1982). This unidirectional water flow thus has a feeding and respiratory function (Randall 1972).

Feeding Mechanisms of the Adults of Parasitic Species

The ability of the adults of parasitic species to attach themselves to, and feed on, their hosts is facilitated by their possession of a large suctorial disc and tongue-like piston, which both possess prominent teeth (Figs. 3.1, 3.2, 3.15, 3.16). The adults of some parasitic species feed on the blood of their hosts, and those of the other species ingest mainly flesh or both blood and flesh (Renaud et al. 2009a) (see ecology section). Although these interspecific dietary differences are reflected in conspicuous differences in the dentition and other feeding structures, the fundamental components of that apparatus are the same in all Lampreys (Potter & Hilliard 1987; Potter & Gill 2003). The feeding apparatus provides, however, not only an example of an extreme form of specialization for a unique form of feeding but also many of the major characters used in Lamprey taxonomy, and the suctorial disc even plays a pivotal role in nest building and mating (Hardisty & Potter 1971b; Hubbs & Potter 1971).

After the adult Lamprey has attached itself to a host by means of its suctorial disc, the teeth on that disc and the supraoral and infraoral laminae (Fig. 3.2) immediately become embedded in the host tissue, thereby enhancing the strength of the attachment. The piston then rocks backward and forward with the result that the teeth on

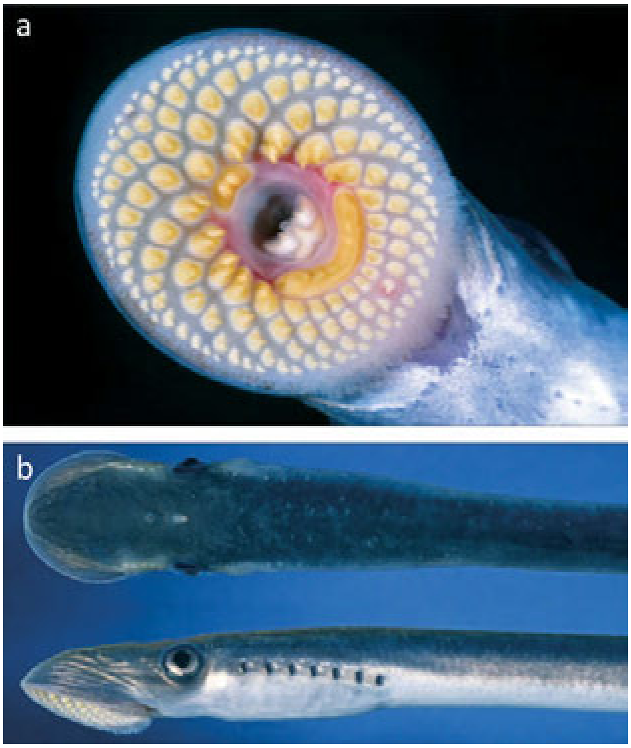

Figure 3.15. (a) Oral disc, and (b) dorsal and lateral views of the anterior region of an anadromous Sea Lamprey, *Petromyzon marinus*, which has just commenced its parasitic phase.

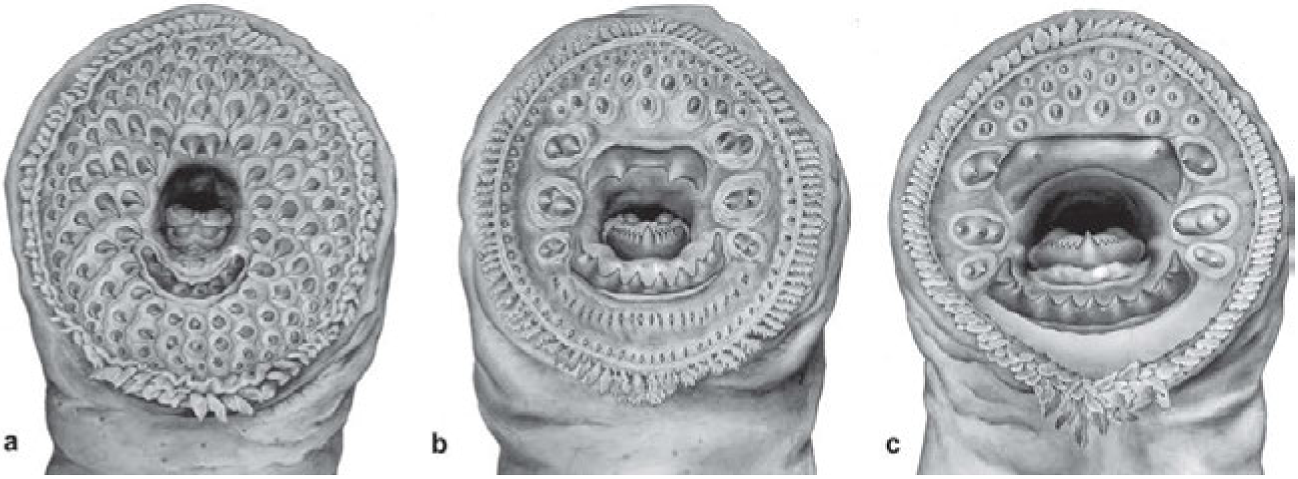

Figure 3.16. Oral discs of (a) the Silver Lamprey, *Ichthyomyzon unicuspis*, which feeds on blood as an adult, and (b) the Arctic Lamprey, *Lethenteron camtschaticum*, and (c) the Western River Lamprey, *Lampetra ayresii*, which both feed on flesh as adults. Permission granted by Fisheries and Oceans Canada; reproduced from V. D. Vladykov and E. Kott. 1979. List of Northern Hemisphere Lampreys (Petromyzonidae) and their distribution. Fisheries and Oceans Miscellaneous Special Publication 42. Reproduced with the permission of © Her Majesty the Queen in Right of Canada, 2010.

its single transverse and two longitudinal laminae destroy the host tissue through rasping, gouging, or both (Potter & Hilliard 1987; Potter & Gill 2003; Renaud et al. 2009a). Lamphredin, a substance with anticoagulant and lytic properties, is secreted onto the host tissue, preventing blood coagulation and aiding in the digestion of the host tissue (Lennon 1954; Baxter 1956; Renaud et al. 2009a). In Northern Hemisphere Lampreys and *G. australis*, this substance is secreted by bean-shaped buccal glands located in the basilaris muscle to either side of the piston and immediately below the eyes. The movement of the piston and its tooth-bearing laminae then help transfer the food backward into the esophagus and eventually the intestine. The presence of velar tentacles at the entry to the water tube, which is located at the anterior end of the esophagus and leads to the branchial pouches, prevents food from entering those pouches (Fig. 3.17).

Blood feeders, such as *P. marinus* and species of *Ichthyomyzon*, possess alate rows of teeth throughout the anterior, lateral, and posterior fields of their suctorial disc, a small and simple supraoral lamina, a W-shaped transverse lingual lamina and two longitudinal lingual laminae that bear fine, sharp teeth (Figs 3.2, 3.15, 3.16a). Blood-feeding Lampreys attach themselves to locations where the vascular supply of the host is well developed, sometimes remaining on the same region for a long period (Lennon 1954). They typically produce a small hole in their hosts with the wound sometimes becoming extended as the Lamprey moves its position (Figs. 3.18, 3.19; Potter & Beamish 1977; King 1980). Their two buccal glands are large, but their velar tentacles are small and few in number (Renaud et al. 2009a).

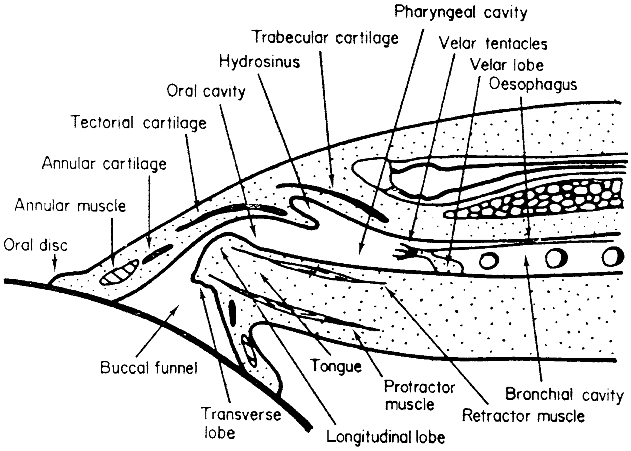

Figure 3.17. Sagittal section through the head of a Lamprey (reprinted from *The Biology of Lampreys*, Vol 1, M. W. Hardisty and I. C. Potter, eds., M. W. Hardisty and I. C. Potter, The General Biology of Adult Lampreys, pages 127–206, 1971).

In contrast to blood-feeding species, those Lampreys that feed on flesh, such as *L. ayresii* and *L. camtschaticum*, remove large chunks of host tissue (Fig. 3.20) and possess a larger and more complex supraoral lamina, and their alate tooth rows are confined to the anterior field of the suctorial disc (Fig. 3.16bc). Flesh-feeding Lampreys also possess smaller buccal glands but larger and more numerous velar tentacles. Further, their transverse lingual lamina is U-shaped and has a greatly enlarged central cusp (Fig. 3.16bc; Potter & Hilliard 1987; Gill et al. 2003; Potter & Gill 2003; Renaud et al. 2009a). The presence of far less dentition on the suctorial disc of flesh feeders than blood feeders enables such Lampreys to alter their position readily after they have removed flesh from one location. During feeding, the lateral cusps of the large blade-like supraoral

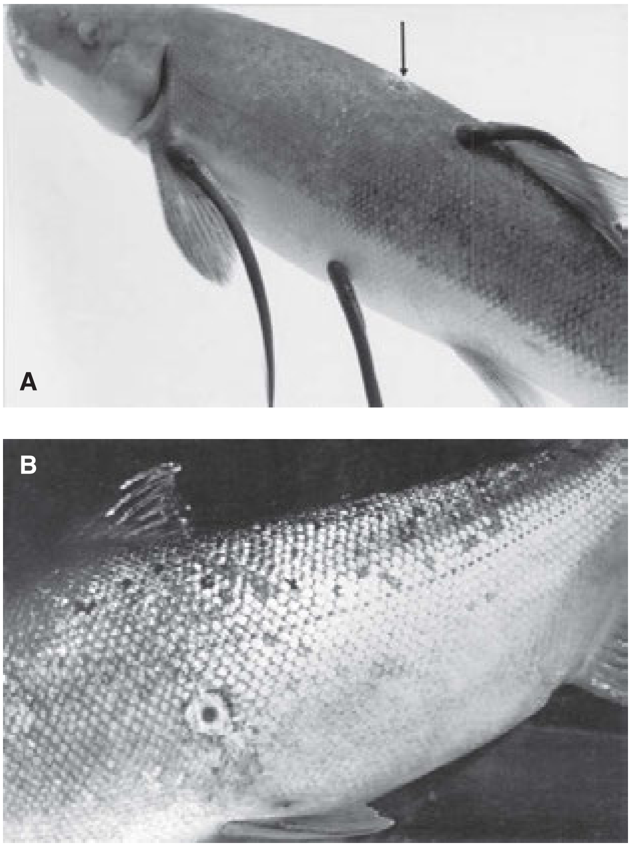

Figure 3.18. (A) Landlocked Sea Lampreys, *Petromyzon marinus*, attached to a White Sucker, *Catostomus commersonii*, and (B) the round and prominent, recently formed wound and a healing wound (just above the pelvic fins) that were produced by anadromous *P. marinus* on an Atlantic Salmon, *Salmo salar* (reproduced with permission of John Wiley & Sons from Potter, I. C., and F. W. H. Beamish. 1977. The freshwater biology of adult anadromous Sea Lampreys *Petromyzon marinus*. Journal of Zoology, London 181:113–130).

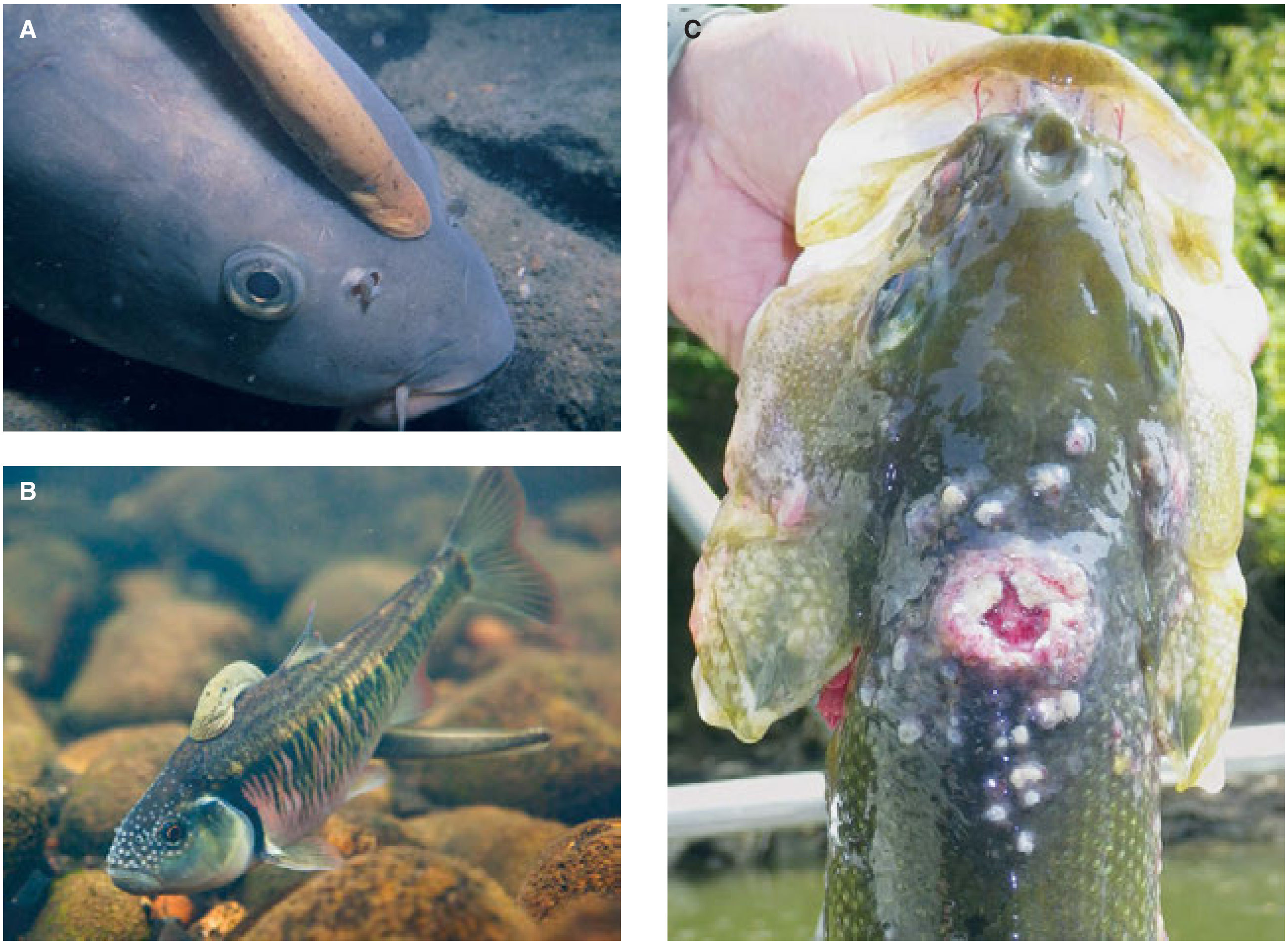

Figure 3.19. (A) Chestnut Lamprey, *Ichthyomyzon castaneus*, attached to the head of a Common Carp (*Cyprinus carpio*) in a clear stream in the Ozark region of Missouri (photograph by and used with permission of W. N. Roston). (B) An unidentified parasitic Lamprey attached to the dorsum of a breeding male Striped Shiner, *Luxilus chrysocephalus*, in the Ocoee River, Polk County, Tennessee (photograph by and used with permission of Jeremy Monroe of Freshwaters Illustrated). (C) Lamprey wound on the nape of a Largemouth Bass, *Micropterus salmoides*, in the Sipsey Fork Black Warrior River drainage, Alabama. The wound is presumably from a Chestnut Lamprey, the only parasitic species known in Mobile Basin (Boschung & Mayden 2004) (photograph courtesy of Andy Dolloff of USDA Forest Service).

remain embedded in the host and interact with the teeth on the lingual laminae to cut away flesh (Potter & Hilliard 1987; Potter & Gill 2003; Renaud et al. 2009a). The insertion and subsequent retraction of the large central cusp on the transverse lingual lamina play a major role in gouging out flesh and passing it backward into the oral cavity. Species such as *T. spadiceus*, which feed on substantial amounts of blood and flesh, possess features that are more similar to those of flesh feeders than blood feeders, such as their possession of a wide supraoral lamina and numerous large velar tentacles (Gill et al. 2003; Renaud et al. 2009a).

The possession of larger buccal glands by blood feeders than flesh feeders presumably reflects a greater need to prevent the blood from clotting and thereby ensure a constant supply of food (Renaud et al. 2009a). The larger and generally more numerous velar tentacles in flesh feeders than blood feeders is related to flesh feeders having a greater requirement to prevent solid material from entering the branchial chamber, where it could clog the gills and restrict respiration (Potter & Gill 2003; Renaud et al. 2009a).

The efficiency of the suctorial mechanism in enabling adult Lampreys to attach to their hosts, and for some species to remain on that host for many hours (Lennon 1954), relies on the well-developed annularis muscles and the strong annular cartilage to which they are attached (Rovainen 1982). Suction is enhanced by the mucus that is secreted by the numerous fimbriae that line the rim of the oral disc (Figs 3.2, 3.15, 3.16; Lethbridge & Potter 1979; Khidir & Renaud 2003). The imprints made by the various dentitional components of an adult of *E. tridentatus* on the operculum of a Chum Salmon (*Oncorhynchus keta*) to which it had attached (Fig. 3.21) attests to the pressure that Lamprey dentition imposes on its hosts.

The evolution of a suctorial disc was accompanied by the development of structures and mechanisms that enabled the respiratory flow to become tidal (i.e., allow water to pass directly into and out of the branchial chamber via the branchiopores). This contrasts with the situation in ammocoetes and all other fishes in which the respiratory flow of water is unidirectional, passing through the oral aperture or mouth into the pharynx and over the gills and out through the vertical gill slits (Randall 1972).

Metamorphosis

From the previous description of larval and adult stages, the metamorphosis of the parasitic species of Lampreys clearly involves radical changes in morphology (Potter 1980a; Youson 1980, 1988, 2003). These changes include a loss of larval structures, such as the oral hood and endostyle, which are adaptations for microphagous feeding, and the development of structures such as well-developed fins, eyes, suctorial disc, and teeth (Figs. 3.1 and 3.2) that facilitate a more active and predatory-parasitic lifestyle.

Although each nonparasitic species, which during metamorphosis is often indistinguishable from that of its parasitic ancestor, does not feed after the commencement of metamorphosis, it undergoes the same changes as parasitic species, reflecting its origins from such a species. Adult characteristics, however, such as teeth and longitudinal folds in the intestine, do not become as well developed as in their parasitic ancestor, and their eyes and oral disc are relatively smaller (Bird & Potter 1979ab; Hilliard et al. 1983; Docker 2009). Further, unlike the situation in parasitic species, the gonads of nonparasitic species start to develop rapidly before the end of metamorphosis, and sexual maturity is attained within a year of the completion of the larval phase (see phylogenetic relationships section). Moreover, the maturation of the gonads is accompanied by the degeneration of the intestine as occurs in parasitic species as their gonads mature during the upstream migration (Hilliard et al. 1983).

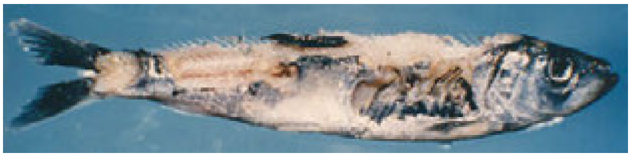

Figure 3.20. The devastating results of an attack by the Western River Lamprey, *Lampetra ayresii*, on a Pacific Herring, *Clupea pallasii*, of 20 cm TL (photograph by and used with permission of R. J. Beamish).

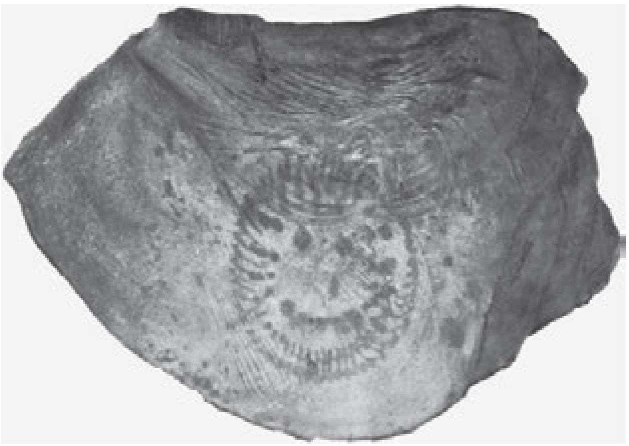

Figure 3.21. The marks made by the various dentitional components of a feeding-phase Pacific Lamprey, *Entosphenus tridentatus*, on the operculum of Chum Salmon, *Oncorhynchus keta*, to which this Lamprey had attached. Note that the operculum has been oriented so that the marks made by the infraoral lamina are located at the bottom of the figure (permission granted by the Canadian Museum of Nature).

GENETICS

Karyology

The Northern Hemisphere Lampreys have an exceptionally large number of small chromosomes. Thus, 8 species from 4 genera (*Petromyzon*, *Ichthyomyzon*, *Lethenteron*, and *Lampetra*) have modal diploid numbers of about 164 with most chromosomes being minute and acrocentric (Howell & Denton 1969; Howell & Duckett 1971; Robinson et al. 1974; Potter & Robinson 1981). Because cephalochordates have 36–38 chromosomes that are likewise small and have their centromere located near or at the end of the chromosomes (Wang et al. 2003), the high diploid number in Lampreys probably arose through polyploidy, a view proposed by Ohno et al. (1968) on the basis of chromosomal data for one species of Northern Hemisphere Lamprey. *Geotria australis*, the sole representative of the Southern Hemisphere Geotriidae, has an even slightly higher diploid number (about 180) with most of the chromosomes also being acrocentric (Robinson & Potter 1981). In contrast, the parasitic *M. mordax* and its nonparasitic derivative *M. praecox*, representing the Mordaciidae, the other Southern Hemisphere family, both have a far lower diploid number of 76, and their chromosomes are metacentric or sub-metacentric (Potter et al. 1968b; Robinson & Potter 1969), suggesting that extensive centric fusions have taken place during the evolution of *Mordacia*. The possibility that such centric fusions occurred within a chromosomal complement similar to that of other Lampreys is consistent with the similarity in the nuclear DNA contents of *M. mordax* and other Lampreys (Robinson et al. 1975).

Lamprey Genetics in Studies of Craniate Evolution

Ohno (1970, 1999) proposed that the diversity, success, and increased complexity of the vertebrates (compared with urochordates and cephalochordates) were related, at least in part, to genome duplications that had occurred during their evolution. He argued that by increasing the number of copies of a gene, the chances of an individual gaining a beneficial mutation would be increased (i.e., natural selection would have more material on which to act). The majority of studies aimed at elucidating the timing of these duplications and the ways that major morphological novelties have arisen within the vertebrates have compared specific genes and their morphological expression in the urochordates, cephalochordates, or both with those in gnathostomes (reviewed by Holland 1999, 2003; Shimeld & Holland 2000). The results of studies, which have included Lampreys, Hagfishes, or both, suggested that at least one and possibly two genome duplications took place in a common ancestor of the agnathans and gnathostomes (Sharman & Holland 1998; Neidert et al. 2000; Kuraku et al. 2008; Putnam et al. 2008). These genomic duplications were followed by further lineage-specific genomic modifications. The characterization of some of the resulting gene families, their link to developmental pathways, and their phenotypic characteristics are increasing our understanding of the evolution of the vertebrates. For example, studies of the *Hox*, *Sox*, *Pax*, and *Dlx* families of genes are providing insights into the development of the neural crest, placodes, endoskeleton, and brain, which are innovations that define the vertebrates (Neidert et al. 2001; Ota et al. 2007; Sauka-Spengler & Bronner-Fraser 2008). Likewise, those of the opsin (Lamb et al. 2007) and Ikaros families (Haire et al. 2000; Rolff 2007) are extending our knowledge on the evolution of the visual systems and the acquired-adaptive immune response, respectively. Indeed, Rolff (2007) suggested that genome duplications led to an imbalance in the genome, a probable underlying cause of cancer, and that this in turn probably resulted in the development of the acquired-adaptive immune system in vertebrates.

The nuclear genome of *P. marinus* undergoes a dramatic remodeling during embryonic development, resulting in the elimination of hundreds of millions of base pairs (and at least one transcribed locus) from many somatic cell lineages (Smith et al. 2009a). This corresponds to a reduction in genome size of >20% between germline (sperm) and soma (blood), which is far greater than has thus far been found in gnathostomes. In the context of the phylogeny of the early vertebrates, it is interesting that the genomes of the other extant agnathan group, the Hagfishes, also undergo similar large-scale rearrangements, involving the removal of repetitive sequences and chromosomes from their germlines (Goto et al. 1998; Kubota et al. 2001; Kojima et al. 2010). Lampreys and Hagfishes thus represent ideal candidates for studies aimed at increasing our understanding of the mechanisms that regulate remodeling of the vertebrate genome and providing an insight into the factors that promote stability and change in that genome (Smith et al. 2009a).

Gene Order

The organization of the genes in the mitochondrial genomes of the Northern Hemisphere Lampreys *P. marinus* and *L. fluviatilis* differs from those of other vertebrates, including the Inshore Hagfish, *Eptatretus burgeri* (Delarbre et al. 2000, 2002). Although this raises the distinct possibility that the gene order in extant Lampreys is unique, the validity of such a generalization requires confirmation that those in the two Southern Hemisphere families of Lampreys (Geotriidae and Mordaciidae) are similar to that of their Northern Hemisphere counterparts.

PHYSIOLOGY

Descriptions of aspects of the physiology of Lampreys are provided in other sections of this chapter when they help account for the behaviors of a particular stage in the lifecycle of Lampreys. In this section, the focus is on respiration, osmoregulation, and vision.

Respiration

In a respirometer, the oxygen consumption by larval *L. planeri* in chambers supplied with a glass bead substrate into which the ammocoetes burrowed was compared with that in chambers without the substrate (Potter & Rogers 1972). The rate of oxygen consumption was greater when ammocoetes were not burrowed than when burrowed, which is the typical, and thus presumably less stressful, situation for ammocoetes (Potter & Rogers 1972; Wilkie et al. 2001). As would be expected with a poikilotherm, the routine (resting) rate of oxygen consumption of burrowed ammocoetes is related to temperature with the mean rates in larvae of *I. greeleyi*, e.g., ranging from 8.1 μl g^{-1} h^{-1} at 3.5°C to 90.1 μl g^{-1} h^{-1} at 22.5°C, which represents a Q_{10} of 3.6 (i.e., rate of change in consumption for each 10°C change) (Hill & Potter 1970). Because the ammocoetes exhibited little or no movement when burrowed, the above routine rates of oxygen consumption were considered to approximate standard rates of oxygen consumption. This conclusion is consistent with the rate of oxygen consumption by the burrowed ammocoetes of *I. greeleyi* at 15°C not being significantly different from the standard rate of oxygen consumption recorded at the same temperature for ammocoetes of *P. marinus* (i.e., by extrapolating oxygen consumption at different swimming speeds to that at zero swimming speed) (Holmes & Lin 1994).

Following vigorous exercise, the rate of oxygen consumption in ammocoetes of *P. marinus* at 15°C increased by 5–6 times, and although subsequently declining progressively, remained elevated for the next 3 h (Wilkie et al. 2001). When larval *P. marinus* are swimming at the maximum rate they can maintain for a prolonged period at a series of temperatures, the relationship between rate of oxygen consumption and temperature is unimodal with the metabolic rate being greater at 15 and 20°C than at 7, 10, and 25°C (Holmes & Lin 1994). The estimated maximum scope for activity (i.e., the difference between standard and active metabolic rates) of larval *P. marinus* in summer is 19°C, which is close to the estimated preferred summer temperature of 20.8°C (Holmes & Lin 1994).

In laboratory trials, the ammocoetes of *I. greeleyi* tolerated greatly reduced oxygen tensions, a particularly valuable trait for an animal that lives an essentially sedentary life in burrows where oxygen tensions are often likely to be low (Potter et al. 1970). For example, larval *I. greeleyi* can tolerate for ≥4 days oxygen tensions of only about 8 mm Hg at 5°C and about 18 mm Hg at 22.5°C. Further, these ammocoetes do not emerge from their burrows until oxygen tensions have declined to near lethal levels. The ability of ammocoetes to tolerate low oxygen tensions is a product of their relatively low metabolic rate and the high affinity of their blood for oxygen (Potter et al. 1970; Potter & Rogers 1972; Bird et al. 1976).

Ammocoetes can use anaerobic metabolism of muscle glycogen to help fuel vigorous muscle activity (Paton et al. 2001; Wilkie et al. 2001). Yet, such activity can only be undertaken in bursts due to the rapid and substantial acidosis produced by the hydrolysis of adenosine triphosphate (ATP) (Hochachka & Mommsen 1983). Glycogen is replenished, however, within 0.5 h of the cessation of exercise and lactate returns to resting levels within an additional 0.5–1.5 h. The ability to recover rapidly from vigorous anaerobic metabolism is invaluable to an animal that relies mainly on such metabolism at those times when it has repeatedly to undertake the energy-demanding task of burrowing (e.g., when the substrate in which it lives is disturbed, such as through scouring during floods).

The standard rate of oxygen consumption in the parasitic species *L. fluviatilis* changed little during the early stage of metamorphosis but then doubled toward the end of that radical change in morphology and physiology (Lewis & Potter 1977). These trends were paralleled during the metamorphosis of the derivative nonparasitic species with the rate of oxygen consumption subsequently remaining high in mature adults. In the case of adult landlocked *P. marinus*, the standard rates of oxygen consumption, derived from swimming-chamber measurements, ranged from 53 mg kg^{-1} h^{-1} at 5°C to 114 mg kg^{-1} h^{-1} at 20°C, and active oxygen consumption at 10°C was 475 mg kg^{-1} h^{-1} (F. W. H. Beamish 1973). These rates, which are comparable with those recorded for salmonids (Trouts and Salmons) of similar weight at a similar temperature, are facilitated in part by the possession of gills with a large surface area (Lewis & Potter 1976ab). Further, because the oxygen dissociation curve of whole blood of adult Lampreys shifts well to the right of that of the ammocoete measured under the same conditions, the oxygen delivery pressure to the tissues is far greater in adults, which would be of benefit to this more active stage in the lifecycle (Bird et al. 1976; Macey & Potter 1982). The shift in the oxygen dissociation curve between ammocoete and adult reflects the change from larval to adult hemoglobins that occurs during metamorphosis (Manwell 1963; Potter & Nicol 1968) and parallels the types of change that take place in amphibians during their metamorphosis and in mammals at about the time of birth (Maclean & Jurd 1972). The shift in the properties of the blood of Lampreys during metamorphosis is coincident with the site of hemopoiesis changing from the intestinal typhlosole and nephric fold in the ammocoete to the fat column above the nerve cord in the adult (Percy & Potter 1976).

As with the ammocoete, the adult Lamprey uses anaerobic metabolism of muscle glycogen to help fuel vigorous exercise, and its glycogen levels can likewise recover rapidly (Boutilier et al. 1993; Mesa et al. 2003). Although glycogen does not recover as rapidly as in ammocoetes, recovery is still faster than is typically the case in teleosts (Boutilier et al. 1993). This rapid recovery would be particularly useful to an animal that swims in bursts, especially when faced with high water velocities and obstacles (Beamish 1974; Mesa et al. 2003; Dauble et al. 2006), and because of its relatively poor swimming performance, depends on anaerobic metabolism of glycogen to help fuel such spurts. The excretion of metabolic acid is the primary means of correcting the extracellular acidosis that follows vigorous exercise (Wilkie et al. 1998). The inferior swimming ability of adult Lampreys, at least compared with many teleosts, is probably related to the absence of a hydrostatic organ and paired fins and the use of a tidal rather than a unidirectional flow of water for respiration (Randall 1972; Beamish 1974). Further, because it generates far greater lateral forces and drag, the sinusoidal mode of locomotion used by Lampreys is less efficient than that of those teleosts in which propulsion is achieved mainly by caudal fin thrust (i.e., subcarangiform, carangiform, or thunniform swimming modes) (Helfman et al. 2009). The adult Lamprey overcomes its limitations in swimming performance by swimming in short bursts and using its oral disc at intervals to attach to rocks or other hard structures to avoid the need to keep swimming to maintain position (Quintella et al. 2009).

When considering aerobic respiration, it is important to recognize that Lamprey hemoglobins, like those of Hagfishes but unlike those of gnathostomes, do not form stable tetramers, dissociating to monomers on oxygenation and associating to dimers or higher oligomers on deoxygenation (Nikinmaa 2001). Monomers have a greater affinity for oxygen than the dimers or oligomers, and are characterized by an oxygen dissociation curve that is parabolic rather than sigmoidal and is shifted farther to the left (i.e., has a lower P_{50}). It is also relevant that, during hypoxia, the red blood cells swell, which leads to a reduction in the mean cellular hemoglobin concentration (MCHC) and thus a trend for dimeric and oligomeric hemoglobins to be converted to monomeric hemoglobins. The increase in the Bohr effect (i.e., shift of the oxygen dissociation curve to the left) that accompanies hypoxia also contributes to an increase in oxygen affinity (Nikinmaa 2001). These characteristics of their hemoglobins provide Lampreys with the dual ability of maximizing the uptake of oxygen under hypoxic conditions and offloading oxygen during vigorous exercise, such as swimming and burrowing, when oxygen is abundant.

Osmoregulation

One of the most conspicuous physiological differences between the two groups of living agnathans is that Lampreys are iono- and osmoregulators, but Hagfishes are iono- and osmoconformers (F. W. H. Beamish 1980a; Bartels & Potter 2004; Wright 2007). Moreover, the anadromous parasitic species can osmoregulate efficiently in fresh water, when they are ammocoetes or migrating upstream as adults and in sea water during their marine trophic phase.

The efficient osmoregulatory mechanisms evolved by Lampreys enable the sodium and chloride concentrations in their internal milieu to be maintained at levels well above those of fresh water when the Lamprey is in rivers and streams and well below those of full-strength sea water when it is in marine environments (Morris 1972; Beamish et al. 1978). As the osmolality of the serum is far lower than that of sea water, Lampreys probably originally lived in fresh water and only later evolved the marine phase that is characteristic of contemporary anadromous species (Lutz 1975; Hardisty et al. 1989).

When in fresh water, Lampreys, like teleosts, are faced with an osmotic influx of water and an efflux of ions across the body surface (i.e., skin and gills). This problem is overcome by an active uptake of monovalent ions across the gills and the excretion of a copious supply of urine from the kidneys and in the ammocoete also through intestinal resorption of ions from its food (Fig. 3.22). Studies of ion exchange mechanisms in teleosts and in the organs of other vertebrates indicate that the intercalated mitochondria-rich cells in the gills of Lampreys when in fresh water are responsible for the uptake of chloride and that the secretion of hydrogen by these cells facilitates the uptake of sodium by the pavement cells or the intercalated mitochondria-rich cells, which are also located in the gills (Bartels & Potter 2004; Bartels et al. 2009).

When in sea water, adult Lampreys are confronted with the reverse situation to that in fresh water (i.e., they lose water to the environment through osmosis) (Fig. 3.22). Although this loss is compensated for by the swallowing of sea water and by the gut absorbing sodium and chloride, the Lamprey then contains an excess of monovalent ions. This is overcome by excreting these ions via the gills as a near hypertonic solution (Fig. 3.22). This excretion is mediated through the chloride cells, which develop in the gills during metamorphosis and use a secondarily active transcellular transport of chloride to provide the driving force for the passive outward movement of sodium through leaky paracellular pathways between these chloride cells (Bartels & Potter 2004).

The above hypotheses on the osmoregulatory mechanisms used by Lampreys in fresh and sea water are supported by results of cytochemical studies involving ammocoetes and metamorphosed Lampreys (Reis-Santos et al. 2008). Proteins crucial for sodium and chloride uptake in fresh water (carbonic anhydrase and a vacuolar-type H^+-ATPase) are co-localized in cells, whose distribution in the gill epithelium corresponds to those of the intercalated mitochondria-rich cells, but Na^+/K^+-ATPase, a marker for chloride cells in gill epithelia, occurs in groups of cells in the interlamellar region of the gill filaments of metamorphosed individuals, and thus where the chloride cells are located. Further, H^+-ATPase expression is negatively correlated with the external salinity, which is consistent with the observation that intercalated mitochondria-rich cells are no longer present when the metamorphosed Lamprey has entered sea water (Bartels & Potter 2004).

In laboratory experiments, ammocoetes of *P. marinus* cannot osmoregulate when the osmolality of the environment exceeds that of their own sera (about 225 mosmol/kg) and about 50% of ammocoetes die within 24 h of transfer to water of 350 mosmol/kg (Beamish et al. 1978). In contrast, fully metamorphosed individuals of anadromous *P. marinus* can readily acclimate to full-strength sea water and then can maintain their serum osmolality at 260 mosmol/kg. This ability to switch rapidly from hyper-osmotic regulation in fresh water to hypo-osmotic regulation in full-strength sea water is so effective that >80% of fully metamorphosed *P. marinus* can survive direct transfer to full-strength sea water (Potter & Beamish 1977). After *P. marinus* re-enters fresh water on its spawning run, its intestine degenerates, and the chloride cells become covered by the flanges of adjacent pavement cells and undergo apoptosis (Bartels & Potter 2004). Consequently, the animal can no longer osmoregulate in hypertonic environments.

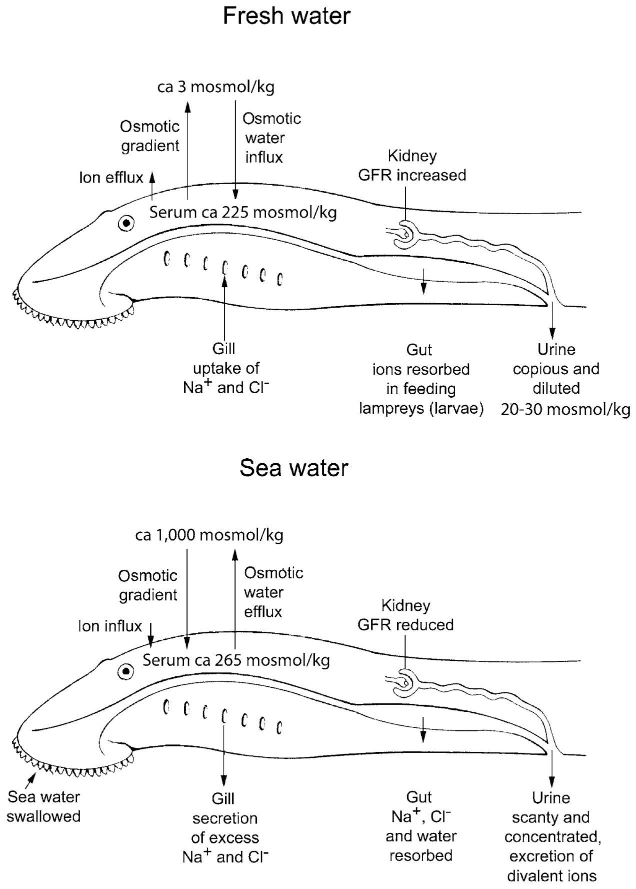
Fresh water
ca 3 mosmol/kg
Osmotic gradient
Osmotic water influx
Ion efflux
Kidney GFR increased
Serum ca 225 mosmol/kg
Gill uptake of Na^+ and Cl^-
Gut ions resorbed in feeding lampreys (larvae)
Urine copious and diluted 20-30 mosmol/kg
Sea water
ca 1,000 mosmol/kg
Osmotic gradient
Osmotic water efflux
Ion influx
Kidney GFR reduced
Serum ca 265 mosmol/kg
Sea water swallowed
Gill secretion of excess Na^+ and Cl^-
Gut Na^+, Cl^- and water resorbed
Urine scanty and concentrated, excretion of divalent ions

Figure 3.22. The osmoregulatory mechanisms employed by anadromous Lampreys during the freshwater (*top*) and seawater (*bottom*) phases in their lifecycles (reproduced with permission from H. Bartels and I. C. Potter. 2004. Cellular composition and ultrastructure of the gill epithelium of larval and adult lampreys: Implications for osmoregulation in fresh and seawater. The Journal of Experimental Biology 207:3447–3462).

Vision

Like most other vertebrates, the eyes of Lampreys are well developed and possess a retina that is specialized for acute vision (i.e., capable of resolving fine detail). Because the eyes of Northern Hemisphere Lampreys possess two photoreceptor types, those Lampreys may have the potential to discriminate prey on the basis of contrast, color, or both (Collin 2007; Collin et al. 2009). In contrast to the eyes of Northern Hemisphere Lampreys, those of *M. mordax* possess a large and single type of photoreceptor, but those of *G. australis* contain five different types. Further, the eyes of *M. mordax* are unique among Lampreys in possessing a tapetum, which would reflect light back toward the photoreceptors, maximizing their capture of light and increasing sensitivity in low light intensities. The eye of *G. australis* is also unique among Lampreys in that it possesses an irideal flap that would reduce the amount of intraocular flare. These interspecific differences are assumed to reflect adaptations to the different modes of life of these two species. Thus, the characteristics of the eyes of adult *M. mordax* are of particular benefit to this species because they are nocturnally active, but those of *G. australis* would be of special value to this species during its adult trophic phase, which is spent in the bright surface waters of the Southern Ocean (Potter & Gill 2003). Although adult Lampreys have well-developed eyes, the dermal photoreceptors that were developed in the ammocoete continue to mediate light avoidance during adult life (Binder & McDonald 2008a).

REPRODUCTION

Lamprey reproduction is a highly synchronized process that is initiated and mediated by a complex neuroendocrine coordination and integration of environmental cues and hormonal mechanisms (Fig. 3.23; Sower 2003). Temperature is a particularly important environmental cue for reproduction. For example, on the basis of a study of *L. planeri* during 14 successive spawning seasons (Hardisty 1961), the spawning of this nonparasitic species was dependent on the attainment of water temperatures of 10–11°C. The hypothalamus plays a major role in controlling reproduction in Lampreys through responding to external and internal cues by the timed release of the decapeptide gonadotropin-releasing hormone (GnRH). As in all vertebrates, GnRH acts on the pituitary to regulate the pituitary-gonadal axis (Fig. 3.23). The pituitary gland responds to GnRH by secreting gonadotropins, which are the major hormones influencing steroidogenesis and gametogenesis; gonadotropins also regulate activities such as spawning behavior (Sower 2003; Sower et al. 2009).

Sexual Dimorphism in Mature Adults

Petromyzontid Lampreys only start to develop sexual dimorphism as they become mature. The mature male possesses a larger suctorial disc and a urogenital papilla and in some species, a small gular pouch. The mature females develop an anal fin-like fold (see Fig. 14 in Hardisty & Potter 1971b; Monette & Renaud 2005).

Upstream Spawning Migration of Parasitic Lampreys

Following the completion of their adult trophic phase, the parasitic species of Lampreys enter rivers and migrate upstream at night to their spawning areas in the headwaters or other areas where the water is relatively shallow (Hardisty & Potter 1971b) (Fig. 3.24). Adults of landlocked *P. marinus* select rivers for their spawning run that contain an extremely potent pheromone, which is released into those rivers by ammocoetes and is not bound by natural organic matter in ways that reduce its natural biological potency (e.g., Sorensen & Vrieze 2003; Fine et al. 2004; Wagner et al. 2009; Fine & Sorensen 2010). This phero-

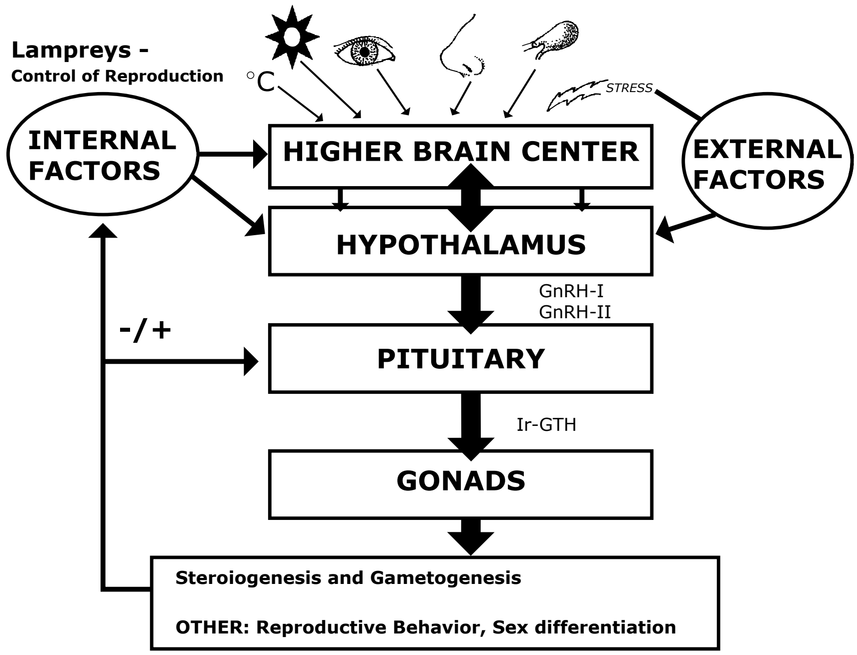

Figure 3.23. Schematic diagram of the hypothalamic-pituitary-gonadal axis in the control of reproduction in the Sea Lamprey, *Petromyzon marinus* (reprinted from Journal of Great Lakes Research 29, Suppl. 1, S. A. Sower, The endocrinology of reproduction in lampreys and applications for male lamprey sterilization, 50–65, 2003, with permission from Elsevier).

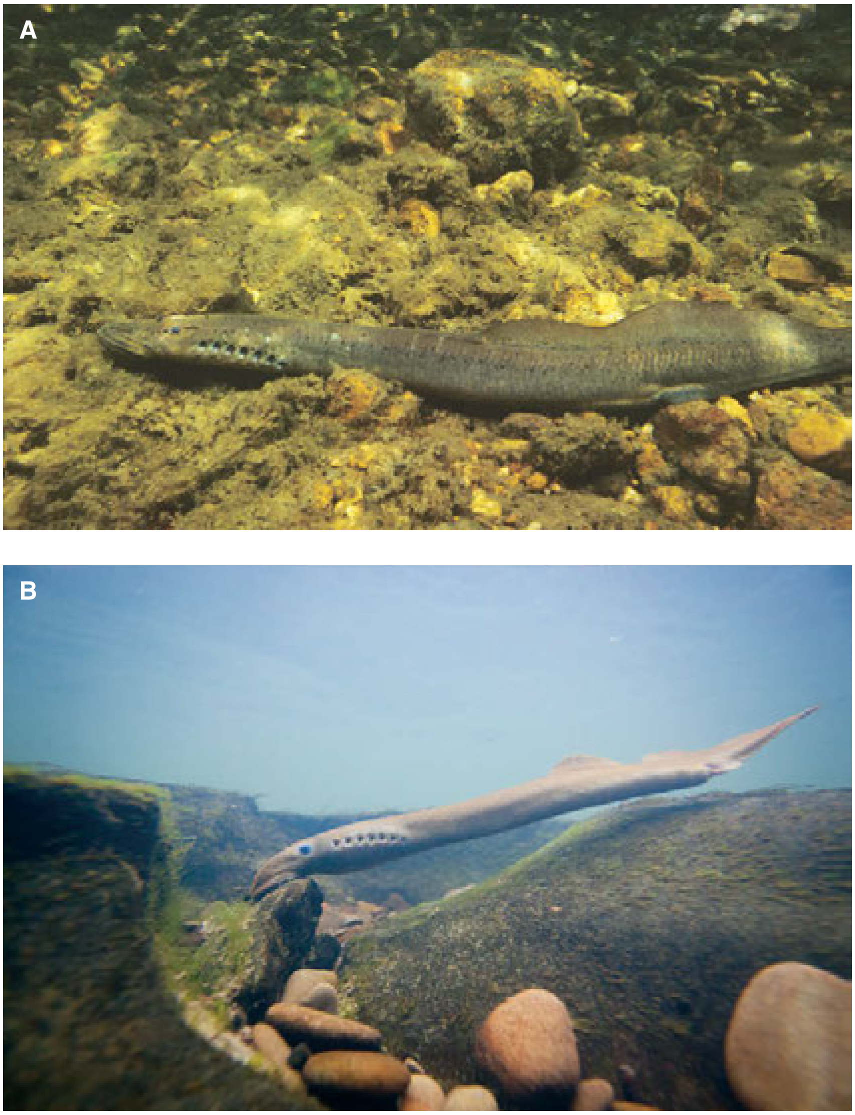

Figure 3.24. (A) Chestnut Lamprey, *Ichthyomyzon castaneus*, a parasitic species, in the midst of moving to its spawning site in Big Creek, Wayne County, Missouri, 10 May 1987 (photograph by B. M. Burr). (B) Pacific Lamprey, *Entosphenus tridentatus*, in its freshwater phase, rests in a swift current as it moves to spawning areas in the Smith River, Douglas County, Oregon (photograph by and used with permission of Jeremy Monroe of Freshwaters Illustrated).

monal attractant comprises a mixture of at least three sulfated steroids, one of which, petromyzonol sulfate, is a Lamprey-specific bile acid derivative (Sorensen et al. 2005; Sorensen & Hoye 2007). These compounds, which induce olfactory and behavioral activity at sub-picomolar concentrations, apparently a record among fishes (Fine & Sorensen 2010), do not appear to be species specific, and their presence in a river presumably indicates to adult Lampreys that suitable Lamprey habitats are present in that river. Indeed, the size of the spawning migrations of landlocked *P. marinus* in the various tributaries of the Great Lakes is positively correlated with the number of larvae resident in those tributaries and thus with the amount of pheromone discharging into the lake (Wagner et al. 2009). Moreover, migrating Sea Lampreys do not enter waters that lack the larval pheromone.

Analysis of the sequence of part of the mtDNA control region of anadromous *P. marinus* from 11 rivers on the Atlantic Coast of North America provided overwhelming evidence that, although Lampreys enter rivers in response to the presence of the pheromone, they do not tend to home into their natal streams (Waldman et al. 2008a). Such a lack of homing, which is consistent with the conclusions from other molecular studies (Rodríguez-Muñoz et al. 2004; Bryan et al. 2005), contrasts with the homing exhibited by many anadromous teleosts. Homing would not be beneficial to parasitic Lampreys because their movements during the adult trophic phase are directed largely by their hosts. This leads to wide dispersal of the adults and consequently a reduction in their likelihood of being close to their natal streams at the end of their parasitic phase when they are preparing to embark on their spawning migration (Waldman et al. 2008a).

Landlocked Sea Lampreys enter rivers when water temperatures in rivers exceed those of their lacustrine environment and subsequent movements occur when water temperatures are >4.5°C and reach their maxima at 10–18.5°C (Applegate 1950). Lampreys do not feed during their upstream migration, and thus their energy requirements must be met largely by the lipid stored during the preceding adult feeding phase (Beamish et al. 1979). During the upstream migration, the intestine degenerates (Youson 1981), and in anadromous species, this and the loss of functional chloride cells in the gills result in their inability to osmoregulate in a hypertonic environment (F. W. H. Beamish 1980a; Bartels & Potter 2004).

The time of onset and duration of the spawning migration varies among species. The upstream migration of the anadromous Sea Lamprey in rivers on the Atlantic Coast of North America commences in May and culminates in spawning in July, and thus lasts for only about 8 weeks (Bigelow & Schroeder 1953b; Beamish et al. 1979). The timing of the spawning run of the landlocked form of *P. marinus* is similar (Applegate 1950). In contrast, the spawning migration of *L. ayresii*, which lasts for about 6 months, commences in September to February and culminates in spawning between April and June (R. J. Beamish 1980). The duration of the spawning run of *E. tridentatus* is even longer than that of *L. ayresii* with the immature adults entering rivers in April to August and not reaching maturity and spawning until the following April to July (R. J. Beamish 1980).

The adults of the landlocked form of *P. marinus* typically migrate upstream at night and use tactile and possibly hydraulic cues, before sunrise, to seek resting places, such as under rocks or the river bank, a behavior that breaks down, however, if suitable refuge cannot be found (Hardisty & Potter 1971b; Dauble et al. 2006; Binder & McDonald 2007). Further, the typical diel pattern of activity exhibited by *P. marinus* during its spawning run is modified by temperature extremes; the animals become inactive at night when temperatures are <7°C and become active during the day when temperatures are >20°C (Binder & McDonald 2008b). Temperature-induced changes in diel activity appear to represent an adaptive behavior that increases the probability that Lampreys will reach their spawning grounds within the narrow thermal range required for successful embryonic development (Binder & McDonald 2008b).

Experimentally blinded individuals of maturing *P. marinus* showed a similar propensity to migrate upstream and at the same rate as control individuals, indicating that vision does not play a role in the behavior of this species during its spawning migration (Binder & McDonald 2007). Indeed, the marked diel pattern of locomotory activity in Lampreys is largely controlled by the synthesis and secretion of melatonin during nighttime by the pineal gland, which forms an essential component of the photoneuroendocrine system that allows Lampreys to measure and keep the time (Korf et al. 1998). Melatonin biosynthesis is regulated by signals from photoreceptors perceiving and transmitting environmental light stimuli and by endogenous oscillators that generate a circadian rhythm that does not depend on any environmental time cue. The over-riding role of the pineal gland in regulating locomotor activity in adult Lampreys is emphasized by the following results obtained from experiments with *L. camtschaticum*. Light-dark entrainment continued in 73% of Lampreys after their eyes had been removed but was completely abolished by subsequent pinealectomy and abolished in most animals that were pinealectomized but had intact eyes (Morita et al. 1992). Further, free-run locomotor activity in constant darkness and animals that had been entrained on a light-dark cycle was abolished by pinealectomy, demonstrating that the pineal plays a crucial role in circadian locomotor activities in Lampreys. The ability of upstream migrating Lampreys to avoid light during the day is facilitated by the presence in their tails of well-developed photoreceptors, which form part of the lateral-line system (Deliagina et al. 1995; Binder & McDonald 2007, 2008a).

When the anadromous *P. marinus* encounters rapid flow during its upstream migration, it alternates short movements of about 67 s duration and periods of rest of about 99 s (Quintella et al. 2009). Further, when this species is faced with difficult passage areas on its spawning run, it spends nearly half of its time attached to the substrate by its suctorial disc, emphasizing that such a use of the disc enables energy to be conserved during this non-trophic period of the lifecycle (Quintella et al. 2009).

The value of the suctorial disc to Lampreys during their spawning run is also demonstrated by the experimental results obtained when upstream migrants of *E. tridentatus* were presented with a 1.4 m vertical weir, thus simulating the type of impediment that Lampreys sometimes encounter on their spawning run (Kemp et al. 2009). The Lampreys used their suctorial disc to gain purchase by attaching to the surface of the weir and launching bursts of modified anguilliform motion. These bursts of ascent, which typically lasted for one-fifth of the total ascent time, were interspersed with stationary attachment using the suctorial disc. The ratio of time spent actively climbing to time spent resting decreased with distance traveled, presumably due to increased fatigue. The ability to successfully complete climbs increased with learning experience, whereby Lampreys adopted more efficient approaches or used easier routes. Adult Lampreys can even circumnavigate obstacles to their upstream migration, such as those produced by dams, weirs, and waterfalls, by moving overland through moist areas, such as those provided in grass and low-lying vegetation, and re-entering the river above the obstacle (Potter et al. 1983). The capacity of upstream migrating Lampreys to survive in moist environments outside the river is facilitated by their ability to extract substantial volumes of oxygen from their environment. In laboratory experiments, the branchial region was responsible for 87% of oxygen uptake and 80% of carbon dioxide excretion by adults of *G. australis* in a moist environment; the gills of these animals presumably retain their integrity in air, continuing to facilitate gas exchange (Potter et al. 1997).

Although adult Lampreys are relatively poor swimmers (Beamish 1974; Dauble et al. 2006), some species cover considerable distances during their spawning run. For example, *E. tridentatus* was caught 400 km upstream from the mouth of the Skeena River (R. J. Beamish 1980). In the case of anadromous *P. marinus*, the energy cost of migrating from the estuary of the St. John River, New Brunswick, to its redds 140 km upstream was estimated to be 300 kcal for males and 260 kcal for females (Beamish 1979). Remarkably, however, this amount of energy use was not as great as that estimated for nest construction and vigorous spawning activities.

The sex ratio of upstream migrant and spawning aggregations of well-established populations of Lamprey species typically ranges from close to parity to a variable excess of males with the proportion of males being greatest in large spawning aggregations (Hardisty & Potter 1971b; Beamish & Potter 1975; F. W. H. Beamish 1980b; Beamish & Austin 1985).

Upstream Spawning Migration of Nonparasitic Lampreys

As they approach maturity, the adults of nonparasitic species emerge from the substrate in which they were burrowed during metamorphosis and undergo a short upstream migration and then spawn and die. The body cavity of females of many nonparasitic species that are about to spawn becomes distended through the presence of the large and fully developed eggs that can sometimes be seen through the body wall (Fig. 3.25). Because nonparasitic Lampreys do not feed after the completion of larval life, the energy they require during metamorphosis, gonadal maturation, and the activities associated with spawning is derived largely from the substantial lipid reserves that are laid down, particularly during the later stages of larval life. In the period between the onset of metamorphosis and spawning in *I. gagei*, lipid and protein were catabolized to such an extent that these two components at spawning had declined to about 7 and 45%, respectively, of their levels at the commencement of metamorphosis (Beamish & Legrow 1983).

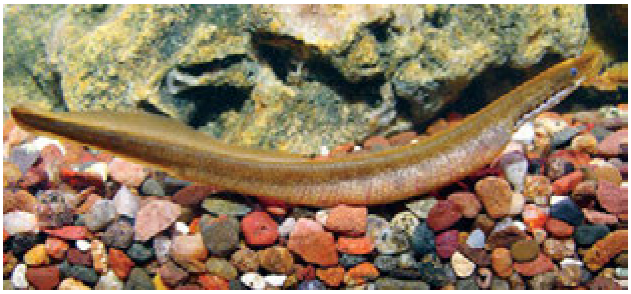

Figure 3.25. Southern Brook Lamprey, *Ichthyomyzon gagei*, showing the abdomen distended with mature eggs (photograph by and used with permission of G. Adams).

Spawning of Lampreys

The spawning behavior of all Lampreys is essentially the same, irrespective of whether they are parasitic or nonparasitic (e.g., Hardisty & Potter 1971b; Mundahl & Sagan 2005; Kucheryavyi et al. 2007). As spawning time approaches, Lampreys become far more active during the day and commence nesting activity. Although spawning typically occurs in late spring or summer, the precise time varies among species according to the critical water temperatures required for spawning activity by those species. For example, in North America, the critical temperature of 22°C for *I. unicuspis* is greater than the 15.5°C for landlocked *P. marinus* and the 10.6–11.1°C for *L. richardsoni* (see Hardisty & Potter 1971b). When spermiating, the males of the landlocked Sea Lamprey release a pheromone (3-keto petromyzonol sulfate) through the gills, which lures ovulating but not pre-ovulating females over hundreds of meters (Siefkes et al. 2005; Johnson et al. 2009).

Most Lamprey species spawn on open gravel substrate in shallow water (Cochran & Gripentrog 1992). The species of *Ichthyomyzon* are atypical, however, in that they often spawn under cover (e.g., boulders, woody debris, vegetation) where current is reduced (Cochran & Gripentrog 1992). This allows these species to reproduce in streams or rivers where the current is too strong in open water areas to allow successful spawning, and it decreases risk from visual predators. Nest construction initially involves the use of the suctorial disc to move stones and thus create a depression. The development of the nest cavity is enhanced by the vigorous activity of the Lampreys that suspends particles in the water column that are then swept downstream (Fig. 3.26). During spawning, which occurs in groups or pairs (e.g., Mundahl & Sagan 2005; Kucheryavyi et al. 2007), the female uses her suctorial disc to attach herself to the larger stones, which are located at the front of the nest facing the direction of water flow and often just upstream of riffles (Fig. 3.26). The male attaches himself to the head of the female and then coils around the female until his urogenital papilla and the cloaca of the female are apposed. The coiling action of the male and the vibrations of the female result in simultaneous emission of eggs and sperm (Fig. 3.27). The fertilized eggs become buried in the substrate, a process facilitated by the disturbance caused to the substrate by the vigor of the spawning activities. *Lethenteron camtschaticum* tends to breed in groups where the current is appreciable (>0.5 m/s) and in pairs when they are in inshore regions of the river where the flow is slower (Kucheryavyi et al. 2007). Further, when *L. camtschaticum* spawns in pairs, the males exhibit agonistic behavior by fighting back other males.

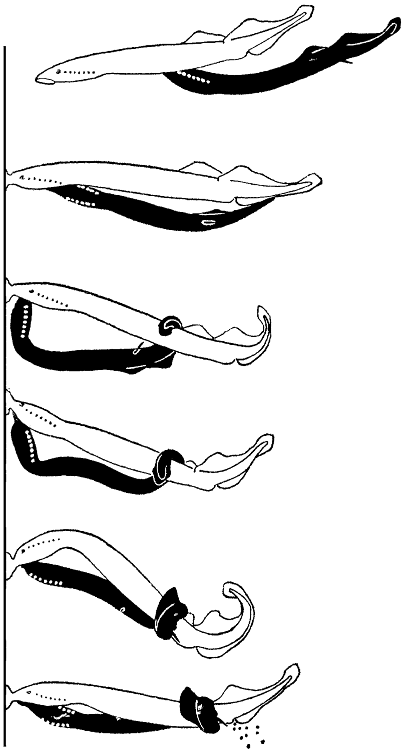

Figure 3.27. The pairing act in Lampreys (reprinted from *The Biology of Lampreys*, Vol 1, M. W. Hardisty and I. C. Potter, eds., M. W. Hardisty and I. C. Potter, The General Biology of Adult Lampreys, pages 127–206, 1971).

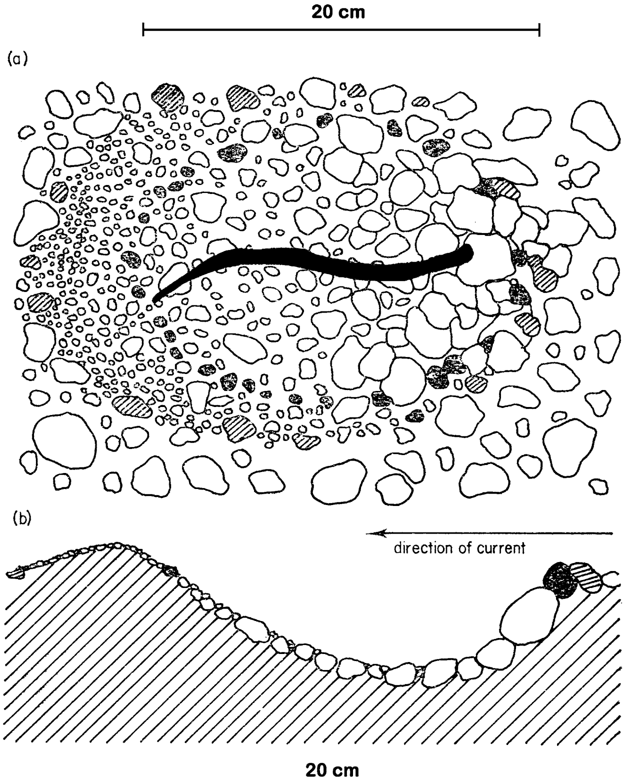

Figure 3.26. Diagramatic representation of a typical brook Lamprey nest. (a) Surface view, and (b) in section (reprinted from *The Biology of Lampreys*, Vol 1, M. W. Hardisty and I. C. Potter, eds., M. W. Hardisty and I. C. Potter, The General Biology of Adult Lampreys, pages 127–206, 1971).

Fecundity

The mature eggs of Lampreys are about 1 mm in diameter, irrespective of whether the species is parasitic or nonparasitic (Hardisty 1964). The fecundity of Lamprey species is related broadly to the body size of their mature adults. Thus, the mean fecundity of large anadromous species, such as *P. marinus*, is about 170,000, compared with 8,000 to 19,000 in smaller species (e.g., the anadromous *L. fluviatilis* and the freshwater parasitic species *I. unicuspis* and *T. spadiceus*) and is typically <3,000 in the nonparasitic and smallest Lamprey species such as *I. fossor*, *T. geminis*, and *L. aepyptera* (see Table 1 in Hardisty 1971).

Embryonic Development

Successful embryonic development through to a viable burrowing prolarva occurs only within a relatively restricted temperature range (15–23°C) (Piavis 1971; Rodríguez-Muñoz et al. 2001). The time from fertilization to hatching in landlocked *P. marinus* and *E. tridentatus* is 10–13 days at 18°C (Piavis 1971; Yamazaki et al. 2003).

ECOLOGY

Larval Phase and Metamorphosis

Ammocoetes spend the vast majority of their time burrowed in the slow-flowing areas of streams and rivers, where the substrate is soft, consists mainly of fine particles, and has a relatively high organic content (Hardisty & Potter 1971a; Beamish & Jebbink 1994; Yap & Bowen 2003). The response to light by photoreceptors in the skin of the tail region ensures that the burrowing movements of ammocoetes continue until the whole animal lies below the substrate surface (Young 1935; Deliagina et al. 1995; Binder & McDonald 2008a). As ammocoetes can potentially be left stranded in their burrows above the water line when water levels recede rapidly following flood events, their ability to survive out of water in moist environments for at least 4 days, apparently through cutaneous respiration, would be of particular advantage to these animals (Potter et al. 1996). The material ingested by larval Lampreys consists of detritus, bacterial mats, diatoms, and other microorganisms with detritus making the greatest contribution to the organic material assimilated at least by the ammocoetes of the landlocked *P. marinus* and *L. appendix* (Moore & Mallatt 1980; Sutton & Bowen 1994; Mundahl et al. 2005). Assimilation of the organic fraction of the diet was >65% (Mundahl et al. 2005).

The species composition of algae ingested by larval *P. marinus* and *La. appendix* was similar to and comparable with those in the sediment and water in the vicinity of the ammocoete's burrow, except in the case of filamentous and epipsammic forms, which were not ingested because of their large size (Moore & Beamish 1973). The times taken for complete evacuation of algal cells from the gut at 16 and 2.5°C were 54 and 70 h, respectively, and 45 and 90% survived passage through the gut in summer and winter, respectively. Ammocoetes of *I. fossor* in oligotrophic streams selectively fed mainly on biofilm fragments that were suspended in the water column (i.e., in the seston) (Yap & Bowen 2003).

The growth and condition of larval Lampreys is related directly to the productivity of their habitats and inversely to the density of the ammocoetes, the latter probably being due in part to the suppressing effects of the release of some chemical or biological agent into the surrounding water (Morman 1987; Morkert et al. 1998; Rodríguez-Muñoz et al. 2003; Yap & Bowen 2003). Further, in the nonparasitic species *I. gagei* and *L. aepyptera* the sex ratios of ammocoetes vary greatly among populations of these species, and the percentage of males increases with larval density (Beamish 1993; Docker & Beamish 1994). This relationship with density and with other environmental variables in the case of *I. gagei* suggests that sex determination is influenced by environmental factors (Beamish 1993).

Because Lampreys do not possess the hard structures whose annuli (rings) are typically used for aging gnathostomatous fishes (e.g., otoliths, vertebrae, fin rays, scales), most estimates of the age compositions of individuals in larval assemblages of single species have relied on tracing modal progressions in length-frequency distributions through sequential samples. These estimates provided overwhelming evidence that the larval phase is protracted and typically lasts for 3–7 years (e.g., Hardisty & Potter 1971a; Potter & Bailey 1972; Beamish & Potter 1975; Beamish & Austin 1985). In the case of the ammocoetes of *I. greeleyi*, oxytetracycline marking indicated that the bands or annuli in their statoliths, a structure analogous to teleost otoliths, were formed each year and could thus be used for aging individuals. Counts of annuli indicated that the larval period of this species is on average relatively long, lasting for 4.2 or 5.2 years (Medland & Beamish 1987). Another elegant study emphasized that the number of annuli in the statoliths of larval landlocked Sea Lampreys often did not accurately estimate the ages of ammocoetes (Dawson et al. 2009). This conclusion was based on comparisons between the known ages of ammocoetes and that estimated from the number of annuli on their statoliths and comparisons involving microsatellite data of the ages determined from statoliths with those based on parental assignment. Dawson et al. (2009) concluded that a combination of bias-corrected ages derived from statolith annuli and length-frequency data substantially increased the accuracy and precision of estimating the ages of ammocoetes. In any assessment of the age composition of larval Lamprey assemblages, however, it should be recognized that, on average and particularly among nonparasitic species, females metamorphose at a larger size and thus at a presumably older age than males (Hardisty 1965; Purvis 1970; Beamish & Austin 1985; Docker & Beamish 1994).

Some of the characteristics exhibited during larval life that influence the timing of metamorphosis were revealed in a series of studies on *P. marinus*. In one of those studies, adults of a landlocked population of the Sea Lamprey were isolated in 1960 in a tributary of the Great Lakes in which they then spawned (Manion & Smith 1978). Tracing of the lengths of the resultant progeny in subsequent years showed that the growth of these ammocoetes was markedly asymptotic and that metamorphosis was size dependent and did not occur in that tributary until the ammocoetes were ≥5 years old (Potter 1980a). Notably, some ammocoetes had not even entered metamorphosis at 12 years old when the study was terminated. Although the regime in this study was in some ways artificial, variability in the age at metamorphosis is almost certainly a characteristic of all Lamprey populations, even if it is less extreme in established populations in reasonably productive rivers.

Petromyzon marinus typically metamorphoses only when a particular condition factor is attained, which in turn, reflects the accumulation of large lipid stores by the body (Lowe et al. 1973; Youson et al. 1979, 1993). Most of these energy reserves, which are required during subsequent months when Lampreys do not feed, are mainly accumulated during a period at the end of larval life when ammocoetes do not increase in length. Nevertheless, when conditions are particularly favorable for growth (i.e., abundant food and low ammocoete densities), individuals in landlocked populations of *P. marinus* do not undergo an arrested growth phase at the end of larval life and can enter metamorphosis after only 2 years of life (Morkert et al. 1998), presumably having accumulated the requisite lipid deposits.

Metamorphosis in Northern Hemisphere species becomes morphologically detectable between early and midsummer (e.g., Potter & Bailey 1972; R. J. Beamish 1980; Youson 1980; McGree et al. 2008). The subsequent internal and external changes involved in the transition from ammocoete to adult are highly synchronized (Youson et al. 1977; Potter et al. 1978; Youson & Connelly 1978; Bird & Potter 1979ab; Hilliard et al. 1983; Holmes et al. 1999; Youson 2004) and at least in the case of *P. marinus*, are stimulated by a rise in water temperature in spring (Youson 2003). In the laboratory, density, starvation, and photoperiod did not stimulate metamorphosis (Youson 2003). The concentration of thyroid hormones in the serum of ammocoetes peaks just before metamorphosis and then declines sharply as metamorphosis is initiated (Lintlop & Youson 1983). This explains why metamorphosis can be induced precociously in Lampreys by the administration of most goitrogens, which inhibit the synthesis of thyroid hormones (Youson 2003). The synchrony of external and internal metamorphic changes implies that the environmental cues and endocrine factors required to initiate metamorphosis are tightly integrated (Youson et al. 1977; Potter et al. 1978; Youson & Potter 1979).

Although Lampreys remain burrowed during metamorphosis, they tend, toward the end of metamorphosis, to move out into faster-flowing areas where the substrate is coarser and oxygen in the interstitial spaces is more likely to be continually replenished (Potter 1980a). When fully metamorphosed, the resultant young adults undertake a largely passive downstream movement, which is highly synchronized, occurs at night, and is initiated by increases in freshwater discharge (Applegate & Brynildson 1952; Potter 1980a). In the landlocked and anadromous forms of the Sea Lamprey, this downstream migration typically peaks in autumn and during flood conditions in the following spring (Hardisty & Potter 1971b; Potter & Beamish 1977).

Ecology of Feeding Adults

In the lacustrine extensions of the large St. John River system, eastern Canada, the young adults of the anadromous form of *P. marinus* that did not migrate downstream in the autumn are prevented from undergoing such a movement during winter and spring because these water bodies are frozen during that period. Thus, in this river, many fully metamorphosed *P. marinus* do not become active until the ice melts in May, but then immediately start feeding on the Alewife (*Alosa pseudoharengus*), American Shad (*Alosa sapidissima*), and White Sucker (*Catostomus commersonii*) (Fig. 3.18a; Potter & Beamish 1977). This enables their lipid reserves and hemoglobin concentrations, which had become greatly depleted during the preceding nontrophic months, to be replenished prior to their migration to the sea (Potter & Beamish 1978; Beamish et al. 1979). After feeding for only 1–2 months at sea, some young adult Sea Lampreys are transported far back into the St. John River by upstream-migrating Atlantic Salmon (*Salmo salar*) to which they have attached (Fig. 3.18b; Potter & Beamish 1977).

During its marine phase, which is estimated to last for 2–2.5 years, the anadromous Sea Lamprey feeds initially on small benthic marine fish species, such as redfishes (*Sebastes* spp.) and the Silver Hake (*Merluccius bilinearis*). As it increases in size, it then targets large and wide-ranging pelagic fishes, such as the Atlantic Mackerel (*Scomber scombrus*), Atlantic Salmon, Swordfish (*Xiphias *gladius*), Bluefin Tuna (*Thunnus thynnus*), and Basking Shark (*Cetorhinus maximus*) and even marine mammals such as the North Atlantic Right Whale (*Eubalaena glacialis*). This results in this Lamprey species becoming widely distributed in the marine environment (F. W. H. Beamish 1980b; Halliday 1991; Nichols & Hamilton 2004). The ability of *P. marinus* to feed on sharks is facilitated by their possession of efficient mechanisms for rapidly excreting the large volumes of urea that are ingested when feeding on elasmobranch blood (Jensen & Schwartz 1994; Wilkie et al. 2004).

The landlocked *P. marinus* feeds parasitically on a number of fish species for 12–20 months, with growth in weight being pronounced and linear between June and September and even increasing in October, after which most individuals were at or approaching the size when feeding ceases and the spawning migration commences in the following spring (Applegate 1950; Smith & Tibbles 1980; Bergstedt & Swink 1995). The above period is shorter than the 18–30 months proposed for the parasitic phase in anadromous *P. marinus* (F. W. H. Beamish 1980b; Halliday 1991), which is consistent with the far smaller maximum size of the landlocked form. The destructive effects of landlocked *P. marinus* on its hosts were an important contribution to the catastrophic decline that occurred in the abundance of the commercially important Lake Trout (*Salvelinus namaycush*) in the upper Great Lakes during the 1940s and 1950s (Smith 1971; Smith & Tibbles 1980). Given that the Lake Trout occupies deep waters, the feeding adults of the landlocked Sea Lamprey apparently prefer relatively low water temperatures. The landlocked Sea Lamprey selectively attacks large Lake Trout but feeds less frequently on and is less likely to kill the more agile Seneca strain than other strains of this species (Schneider et al. 1996; Madenjian et al. 2004) (see commercial importance section).

Like anadromous *P. marinus*, the young adults of *E. tridentatus* begin feeding in either fresh or salt water, sometimes as early as mid-October, only 3–4 months after the onset of metamorphosis (R. J. Beamish 1980). After entering the sea, *E. tridentatus* moves into waters >20 m deep and targets species such as the Sockeye Salmon (*Oncorhynchus nerka*) and Pink Salmon (*Oncorhynchus gorbuscha*), which aggregate in these waters before entering rivers on their spawning runs. When *L. ayresii* enters the sea, nearly a year after the commencement of metamorphosis, it attacks and removes large amounts of flesh from the Pacific Herring (*Clupea pallasii*) and *Oncorhynchus* spp. (R. J. Beamish 1980). The adult parasitic phase of the Pacific Lamprey can last for 3.5 years, but that of the Western River Lamprey is typically completed within 4 months. *Entosphenus macrostomus*, the landlocked derivative of *E. tridentatus*, feeds predominantly on freshwater salmonids and juveniles of the anadromous Coho Salmon (*Oncorhynchus kisutch*) (Beamish 2001).

The three parasitic species of *Ichthyomyzon*, which are all confined to fresh water and attain relatively similar body sizes, feed on a wide range of actinopterygian fishes (Hubbs & Trautman 1937; Hardisty & Potter 1971b; Cochran & Jenkins 1994; Renaud 2002; Cochran et al. 2003; Cochran & Lyons 2004). The hosts of *I. unicuspis* include the Paddlefish (*Polyodon spathula*), Lake Sturgeon (*Acipenser fulvescens*), Northern Pike (*Esox lucius*), and Muskellunge (*Esox masquinongy*). *Ichthyomyzon unicuspis* and *I. castaneus*, which attack similar hosts, feed below the ice during winter (Cochran et al. 2003). The parasitic phase of *I. unicuspis* lasts for about a year with growth occurring mainly in summer (Cochran & Marks 1995).

The adults of *Ichthyomyzon* species typically forage at night, which would enhance their foraging efficiency because they would be less visible than during the day and thus could approach the host more effectively, especially if the host is quiescent at night (Cochran 1986a). Adult Lampreys possess a well-developed olfactory organ and prominent olfactory lobes in the brain, which strongly suggests that they use olfaction when seeking prey (Kleerekoper 1972). This conclusion is consistent with a laboratory study involving adult *P. marinus*, in which the introduction of water in which Lake Trout had been held into their holding tank immediately elicited vigorous activity (Kleerekoper 1972). Under natural conditions in the wild, the adult Lamprey presumably uses olfaction (a relatively long-distance sense) to locate its prey, after which it probably uses its eyes to target the prey more precisely and ensure that it attaches to an appropriate region of the host's body (see physiology section; Farmer 1980).

Blood versus Flesh Feeding

Analysis of the gut contents of adults of the landlocked *P. marinus*, which had fed on Lake Trout and Rainbow Trout (*Oncorhynchus mykiss*) whose red blood cells had been labeled with chromium-51, revealed that blood constituted >98% of the food ingested by this species (Farmer et al. 1975). Inspection of gut contents and hematological tests showed that the food of *I. bdellium*, *I. castaneus*, and *I. unicuspis* also consisted predominantly of blood (Renaud et al. 2009a). In marked contrast to *P. marinus*, which produces a small and often well-defined hole through which body fluids are then extracted (Fig. 3.18), *L. camtschaticum* and *L. ayresii* remove large amounts of flesh from their teleost prey (Fig. 3.20; Nikolskii 1956; R. J. Beamish 1980). *Tetrapleurodon spadiceus* represents an intermediate feeding mode in that it ingests both blood and flesh (Álvarez del Villar 1966; Cochran et al. 1996).

Petromyzon marinus tends to attach to the ventral surface and near the pectoral fins of its host, where scales are reduced, the musculature is thin, and a well-developed vascular supply is nearby (Fig. 3.18), thus optimizing the potential to obtain a plentiful supply of blood (Davis 1967; Potter & Beamish 1977; King 1980; Cochran 1986b). In contrast, the adults of *Ichthyomyzon*, which also mainly ingest blood, tend to attach to the dorsal surface of their hosts in shallow waters (Cochran 1986b; Renaud 2002), where pelagic species are largely absent. Attacks by *I. unicuspis* on the Paddlefish, however, occur in deep water, and the attachment is ventral (Cochran 1986b). *Ichthyomyzon unicuspis* also attaches within the branchial cavity of the Paddlefish, which would provide access to blood under pressure, especially from that in the ventral aorta, and protection from dislodgement during breaching by the Paddlefish (Cochran & Lyons 2010).

Small, recently metamorphosed *P. marinus* often feed on small hosts, whose scales and skin are thinner than those of larger individuals of the same species, but large *P. marinus* and other blood-feeding Lampreys tend to attack large hosts (Cochran & Jenkins 1994; Cochran et al. 2003). The latter tendency is advantageous because a large host is more likely than a small host to survive an attack because it involves the destruction of a relatively smaller part of the body surface. The ability of fishes to recover from attacks by blood-feeding Lampreys is illustrated by the observation that 27% of Muskellunge that had been recently attacked by *I. unicuspis* had healed wounds attributable to earlier Lamprey attacks (Renaud 2002).

Lampetra ayresii and its European counterpart, *L. fluviatilis*, remove large chunks of flesh from the dorsal surface of their hosts, which is the main site of attachment of flesh-feeding species (Fig. 3.20; Bahr 1933; R. J. Beamish 1980; Cochran 1986b). In contrast to blood-feeding Lampreys, flesh-feeding species typically attack small, schooling teleosts, which results in the relatively rapid death of those hosts (Cochran & Jenkins 1994). The abundant pool of prey provided by schooling fish enables flesh-feeding Lampreys to readily find another prey once they have killed their current host.

Parasitism, Commensalism, and Predation

The parasites of *P. marinus*, *I. castaneus*, *E. tridentatus*, *L. camtschaticum*, *L. appendix*, and *L. richardsoni* have been studied in various North American localities (reviewed by Appy & Anderson 1981) with the majority of information being provided by the landlocked form of *P. marinus* in the Great Lakes. Parasites include species belonging to Bacteria (*Pseudomonas* and *Aeromonas* spp.), Fungi (*Saprolegnia* spp.), Protozoa (*Ichthyophthirius* and *Trichodina* spp.), Platyhelminthes (*Diplostomulum*, *Diplostomum*, *Podocotyle*, *Nanophyetus*, *Eubothrium*, *Triaenophorus*, *Phyllobothrium*, and *Proteocephalus* spp.; and larva of monorchiid spp.), Acanthocephala (*Neoechinorhynchus* and *Metaechinorhynchus* spp.), Aschelminthes (*Truttaedacnitis*, *Cystidicola*, and *Eustrongylides* spp.), Annelida (*Pisicola* spp.), and Arthropoda (*Ergasilus* spp.). Although no petromyzontid from North America is documented as host to freshwater unionid mussels, the glochidial stage of the unionid mollusk *Anodontoides ferrussacianus* was found on the gills of landlocked *P. marinus*; however, the metamorphosis of this parasite was not observed (Wilson & Ronald 1967).

The eggs and early larval stages of Lampreys are preyed on by various fishes, including logperches (Percidae), Eels (Anguillidae), minnows (Cyprinidae), Sculpins (Cottidae), Sticklebacks (Gasterosteidae), and trouts (Salmonidae) (Hardisty & Potter 1971a). Adult Lampreys are preyed on in fresh waters by fishes, snakes, birds, and mammals and in the sea by fishes and mammals (Renaud 1997; Cochran 2009).

CONSERVATION

Renaud (1997) and Jelks et al. (2008) reviewed the conservation status of Northern Hemisphere Lampreys and North American Lampreys (Table 3.3), respectively. Fifteen of the 23 North American species (65%) according to Renaud (1997) and 10 of 23 (43%) according to Jelks et al. (2008) were considered at some level of risk (Vulnerable, Threatened, or Endangered) in at least part of their North American range. This difference in percentage values is mainly due to differences in the scale of examination in the two studies. For example, Jelks et al. (2008) did not consider the six species of *Ichthyomyzon* at risk at the continental level, but Renaud (1997) regarded them as at risk at the national or subnational level (states and provinces). Several authors have updated the information on the conservation situation for Lampreys in Canada, California,

Table 3.3. Conservation status of Lampreys in North America according to Jelks et al. (2008).

Taxon	Status	Listing Criteria[1]	NatureServe Global Rank[2]
Entosphenus hubbsi	Threatened	1, 2, 4, 5	G1G2
Entosphenus lethophagus	Vulnerable	1, 5	G3G4
Entosphenus macrostomus	Threatened	5	G1
Entosphenus minimus	Endangered	1, 2, 5	G1
Entosphenus similis	Threatened	1, 5	G3G4Q
Entosphenus tridentatus	Vulnerable	1, 2	G5
E. tridentatus	Threatened	1, 5	G5T1
Goose Lake population			
Lampetra ayresii	Vulnerable	1, 4	G4
Lampetra richardsoni	Not at Risk	Not Applicable	G4G5
L. richardsoni	Endangered	1, 5	G4G5T1Q
Morrison Creek population			
Tetrapleurodon geminis	Threatened	1, 5	Not Applicable
Tetrapleurodon spadiceus	Endangered	1, 2, 5	Not Applicable

[1] 1=habitat destruction; 2=over-exploitation of the species or its host or intentional eradication; 4=predation by nonindigenous species; 5=restricted range

[2] G1=critically imperiled; G2=imperiled; G3=vulnerable; G4=apparently secure; G5=secure; T1=critically imperiled infraspecific taxon; Q=questionable taxonomy

Kansas, and Oregon (Close et al. 2002; Haslouer et al. 2005; Moyle et al. 2009; Renaud et al. 2009b). Summaries of the conservation status of Lampreys in the United States and Canada are updated on an irregular basis on the NatureServe website (NatureServe 2010) and also on a website that includes Mexico, maintained jointly by the U.S. Geological Survey and American Fisheries Society (USGS 2010) (taken from Jelks et al. 2008).

According to NatureServe (2010; Table 3.3), five West Coast endemic taxa (species or infraspecific rank) are either Critically Imperiled (*E. macrostomus*, British Columbia; *E. minimus*, Oregon; Goose Lake population of *E. tridentatus*, Oregon and California; and Morrison Creek population of *L. richardsoni*, British Columbia) or Critically Imperiled / Imperiled (*E. hubbsi*, California). In Mexico, *T. spadiceus* is considered Endangered (Cochran et al. 1996; Jelks et al. 2008). Although the discovery of populations of *E. minimus* (Lorion et al. 2000), a species assumed to be extinct, is encouraging, some species of Lampreys have clearly suffered from deleterious anthropogenic effects and further work on their conservation status is likely to reveal that more populations are at risk. Since 1989, the situation for *E. hubbsi*, *E. macrostomus*, and the Goose Lake population of *E. tridentatus* has deteriorated (Jelks et al. 2008). The major threats remain habitat degradation and the effects of stream regulation, and restricted ranges place West Coast endemics at risk (Table 3.3). In the Laurentian Great Lakes, the continued use of lampricides, as part of the Sea Lamprey Control Program, is affecting the non-targeted native species of Lampreys, and particularly *I. unicuspis*, and is thus also a cause for concern (McLaughlin et al. 2003).

The susceptibility of Lampreys to modifications to rivers is well illustrated by the fact that the anadromous, parasitic *E. tridentatus* can no longer enter Elsie Lake, British Columbia, because the construction of a dam now prevents the downstream and upstream movement of this species (Beamish & Northcote 1989). Although the individuals of the Pacific Lamprey that became landlocked by this barrier fed on resident salmonids in the lake, they did not subsequently reach maturity and spawn. Thus, landlocking of a population of anadromous species of Lamprey does not necessarily lead to the development of a viable population of the landlocked form of that species.

COMMERCIAL IMPORTANCE

Although adult Lampreys are fished commercially in numerous rivers in Europe, their potential as a food source or delicacy has not been exploited widely in North America, and as a consequence, the declines in abundances of the parasitic species have often not been fully appreciated. Native Americans, however, value the Pacific Lamprey so highly that this species is a cultural icon. This led to the initiation of research aimed at developing methods for restoring the populations of *E. tridentatus* at least in the Columbia River basin (Close et al. 2002).

The over-riding economic importance of Lampreys in North America resides in the detrimental effect that they have had on fish populations. A dramatic example of such an effect is provided by the deaths caused to an estimated 60 million juvenile fishes in the Strait of Georgia in 1975 by the attacks of an estimated 667,000 Western River Lampreys (R. J. Beamish 1980). Even more impressive, however, is the fact that, in 1990 and 1991, the same species, which normally attacks the Pacific Herring, killed a minimum of 20 and 18 million Chinook Salmon, *Oncorhynchus tshawytscha*, respectively, and a minimum of 2 and 10 million Coho Salmon, respectively (Beamish & Neville 1995). Overall, in 1991 the Western River Lamprey killed about 65 and 25% of the total Canadian hatchery and wild production of Coho Salmon and Chinook Salmon, respectively, in the Strait of Georgia.

Another striking example of the massive influence of Lampreys on host populations is provided by the destruction caused to fish stocks, and particularly those of the Lake Trout, by the landlocked form of *P. marinus* when it invaded the upper Great Lakes (Smith 1971; Smith & Tibbles 1980; Christie & Goddard 2003). Although the first record of the Sea Lamprey in the Lake Ontario basin dates from 1835, mtDNA analyses strongly indicate that this landlocked form of *P. marinus* is a natural post-Pleistocene colonizer of this large water body (Waldman et al. 2004, 2009); this conclusion, however, has been questioned, (Eshenroder 2009). By the end of the 1800s, records of attacks by Sea Lampreys on Lake Ontario fishes and particularly Lake Trout were numerous.

The Sea Lamprey entered Lake Erie from Lake Ontario in 1919 following the deepening of the Welland Canal between those two lakes, which provided a bypass to the barrier posed by Niagara Falls. *Petromyzon marinus* spread rapidly through the Great Lakes, bringing about rapid declines in, e.g., Lake Trout in Lake Huron between 1935 and 1945, in Lake Michigan between 1945 and 1950, and in Lake Superior between 1950 and 1960. The extreme effects of the landlocked Sea Lamprey on fish populations led to a substantial investment in research, and this resulted, through the detailed studies of Vernon Applegate and his colleagues, in a sound knowledge of the biology of this species in the Great Lakes (Applegate 1950). Since that time, various measures have been introduced to control *P. marinus* in the Great Lakes.

When mechanical and electrical barriers proved ineffective at preventing or killing Lampreys during their migration to spawning areas, attention was turned to using chemical treatments to kill ammocoetes. After testing >6,000 chemicals, 3-trifluoromethyl-4-nitrophenol (TFM) was selected for use. This compound was more toxic to ammocoetes than other aquatic organisms, could be handled readily in the field, was effective at low concentrations, and was relatively inexpensive. TFM was first used in the late 1950s and in the 1960s. A second larvicide, the molluskicide Bayer 73 (2', 5-dichloro-4'-nitrosalicylanilide) enhanced the effects of TFM and was effective on its own when applied directly to the substrate surface. The use of chemical larvicides was successful and led to a substantial reduction in the number of spawning Lampreys. Recognition of the importance of developing more natural and integrated methods of Lamprey control led, e.g., to the testing of sterile male release techniques and the possible application of pheromones to influence migratory and spawning success (Bergstedt et al. 2003; Twohey et al. 2003ab; Johnson et al. 2009). The great relevance of the landlocked Sea Lamprey to the survival of fisheries in the upper Great Lakes is recognized by a huge investment in research and control measures, and the establishment of an Integrated Management of Sea Lamprey (IMSL) plan by the Great Lakes Fishery Commission. For further details of the Sea Lamprey in the upper Great Lakes, the reader is referred to the numerous papers that were presented on this topic at a Sea Lamprey International Symposium (SLIS II) and that were published in a special edition of the *Journal of Great Lakes Research* (2003, vol. 29, Supplement 1).

LITERATURE GUIDE

The four volumes of *The Biology of Lampreys*, edited by Hardisty & Potter (vol. 1, 1971; vol. 2, 1972; vol. 3, 1981; vols. 4 a & b, 1982, Academic Press, London), provide accounts of a wide range of aspects of the biology of Lampreys. The *Proceedings of the Sea Lamprey International Symposia I* and *II*, which were published in special issues of the *Canadian Journal of Fisheries and Aquatic Sciences* (1980, vol. 37) and the *Journal of Great Lakes Research* (2003, vol. 29), provided further information on the biology of Lampreys, and detailed accounts of the invasion, effects, and control of the landlocked Sea Lamprey in the

Great Lakes of North America. A broad, innovative, and easily approachable account of Lampreys was provided by the doyen of Lamprey biology, Martin Hardisty, in his final work entitled *Lampreys: Life without Jaws* (2006). Papers relating to contemporary views on the systematics of Lampreys and of the relationships of the cyclostomes and gnathostomes include Gill et al. (2003), Janvier (2009), Lang et al. (2009), and Near (2009). Several papers on Lampreys, including Margaret Docker's excellent account of paired species, were published in the *Proceedings of the Biology, Management, and Conservation of Lampreys in North America Symposium* in 2009 by the American Fisheries Society edited by Brown et al. (2009). In the Food and Agriculture Organization of the United Nations Species Catalogue entitled *Lampreys of the World*, Renaud (2011) gives an overview of the biology of all species.

Acknowledgments

We are particularly grateful to Professors Helmut Bartels, Max Cake, Phil Cochran, Shaun Collin, Margaret Docker, Peter Holland, and Mike Wilkie for providing very helpful comments and criticisms of those parts of this chapter that covered their areas of expertise. Gratitude is also expressed to Dr. David Bird for providing us with Fig. 3.15, D. Naughton for Fig. 3.21, and to Gordon Thomson and Steeg Hoeksema for producing other figures. We also thank Amy Commens-Carson for redrawing several figures.

Chapter 4 Dasyatidae: Whiptail Stingrays

Michael D. Burns, Carter R. Gilbert, and Melvin L. Warren, Jr.

The Whiptail Stingrays (Dasyatidae) are members of the order Myliobatiformes (Stingrays), a group of 10 families that are included, together with 3 other orders, in the subdivision Batoidea of the class Chondrichthyes (Cartilaginous Fishes) (McEachran & Aschlimann 2004; Nelson 2006). Whiptail Stingrays are members of the superfamily Dasyatoidea, which also includes the families Potamotrygonidae (River Stingrays), Gymnuridae (Butterfly Rays), and Myliobatidae (Eagle Rays).

The Stingrays are cartilaginous and have depressed bodies with greatly expanded pectoral fins forming a disc. The slender tail bears a serrated, venomous spine capable of inflicting serious wounds and causing excruciating pain. Whiptail Stingrays (and other Stingrays) give birth to live young (ovoviviparity) with the young closely resembling the adults. The family name is from the Greek roots *dasyatis*, meaning "shaggy, rough," likely in reference to the hardened portion of the dorsal surface that contains tubercles, thorns, or prickles in some species, and *batis*, meaning "skate," in reference to rajiform fishes. The hypothesized sister-family to Dasyatidae, the River Stingrays (Potamotrygonidae), contains 3 genera, *Paratrygon*, *Plesiotrygon*, and *Potamotrygon* with a total of 20 species across the 3 genera. Additional species may be added to the potamotrygonids pending further research because species within two dasyatid genera (*Taeniura* and *Himantura*) are hypothesized as being more closely related to River Stingrays. River Stingrays occur in South American fresh waters and represent the sole freshwater family of Stingrays. The River Stingrays have a reduced rectal gland weight and reduced urea, both important in osmoregulation in sea water. The River Stingrays are hypothesized to have arisen in the Late Cretaceous (99.6–65.5 mya) or Early Tertiary (65 mya) period (Grande 1980).

DIVERSITY AND DISTRIBUTION

Dasyatis sabina, the Atlantic Stingray, is a member of the largest genus in the family Dasyatidae and is the sole North American freshwater species. The Dasyatidae contain about 68 species in 6 genera: *Dasyatis* (≥38 species), *Himantura* (≥23 species), *Pastinachus* (1 species), *Pteroplatytrygon* (1 species), *Taeniura* (3 species), and *Urogymnus* (2 species) (Compagno 1999a, 2005; Nelson 2006). Of these, 5 genera and 20 species occur in the Atlantic Ocean (Western and Eastern combined, including the Mediterranean Sea) and the Eastern Pacific Ocean. *Pteroplatytrygon violacea*, the Pelagic Stingray (which has a worldwide distribution in tropical and temperate seas), an oceanic species, occurs in all three regions, and *Dasyatis centroura* (Roughtail Stingray) is found in both the Western and Eastern Atlantic Ocean. Adjusting the overall totals to account for the extended distributions of these 2 species, 3 species are limited to the Eastern Pacific (4 total), 6 restricted to the Western Atlantic (8 total), and 9 confined to the Eastern Atlantic (11 total).

The genus *Dasyatis* with ≥38 species is circumglobal in tropical and warm temperate regions, occurring in the Atlantic, Pacific, and Indian Oceans (Table 4.1). A few species of *Dasyatis*, *Himantura*, and the Cowtail Stingray (*Pastinachus sephen*) occur permanently or sporadically in tropical or subtropical freshwater lakes and rivers (Thorson & Watson 1975; Taniuchi 1979; Compagno & Roberts 1982, 1984; Otake 1991; Nelson 2006). The Atlantic Stingray occurs in coastal

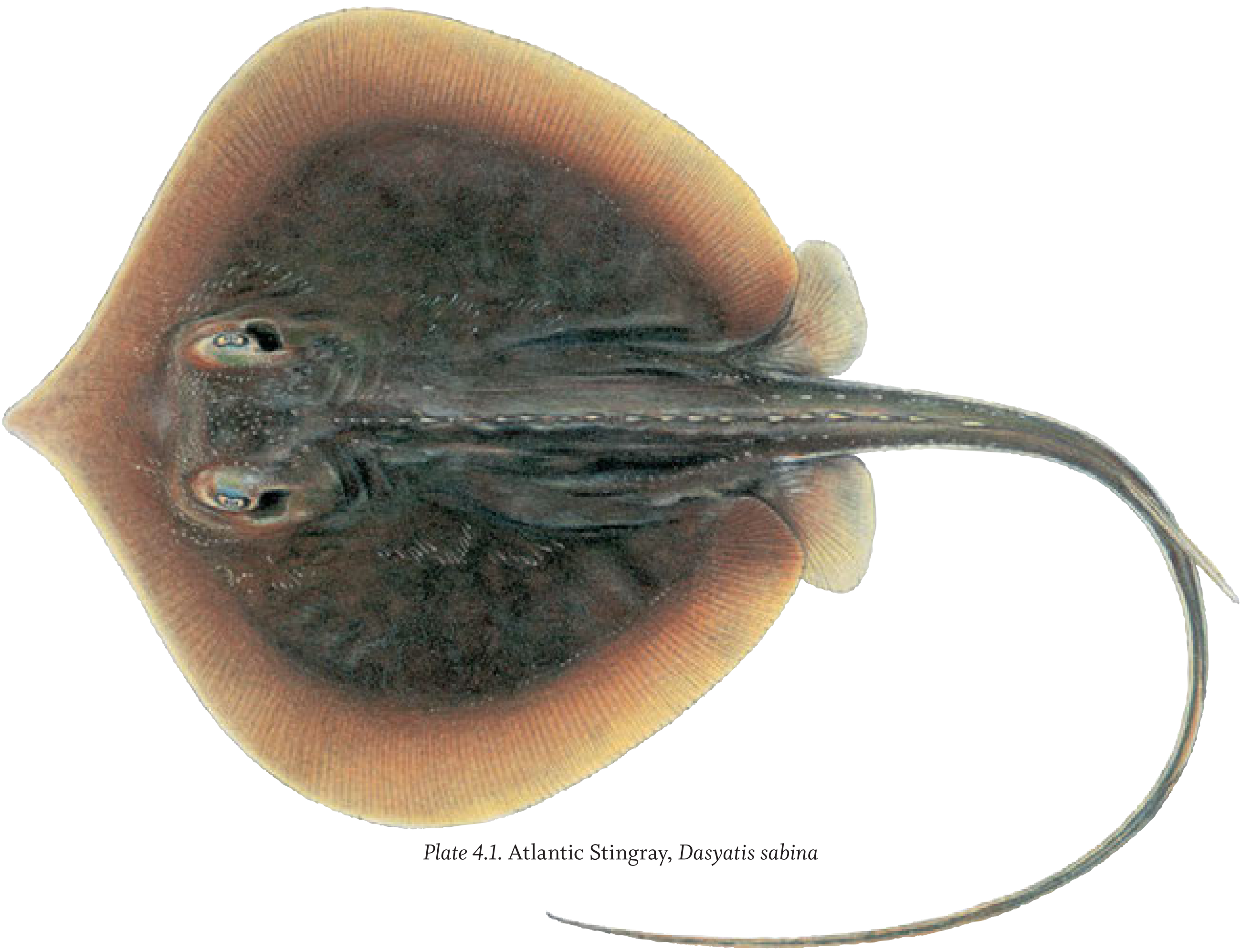

Plate 4.1. Atlantic Stingray, *Dasyatis sabina*

and brackish waters (occasionally in fresh water) in the Atlantic Ocean from Chesapeake Bay south to Florida and in the Gulf of Mexico from Florida to the Campeche Gulf and the tip of the Yucatan Peninsula (Ross & Burgess 1980; Johnson & Snelson 1996). Although most records are from shallow inshore waters (typically <2.4 m deep), an individual was taken off Florida at 203 fathoms (>183 m) (identified by W. C. Schroeder, Harvard Museum of Comparative Zoology, MCZ 51812). No confirmed records exist from the Bahamas (Böhlke & Chaplin 1968), Cuba (contra Duarte-Bello & Buesa 1973), or other insular areas. Alleged occurrences in the Caribbean Sea and southward (Meek & Hildebrand 1923) are based on misidentifications or unverified supposition of occurrence (Bigelow & Schroeder 1953a; McEachran & de Carvalho 2003). The Atlantic Stingray is the only Stingray in North America known to enter fresh water. A reproducing population occurs within fresh water in the St. Johns River system, Florida (Fig. 4.1) (McLane 1955; Tagatz 1968; Johnson & Snelson 1996) (see physiology section).

PHYLOGENETIC RELATIONSHIPS

Higher Relationships

The class Chondrichthyes contains two monophyletic evolutionary lineages, the subclasses Holocephali and Elasmobranchii (Lund & Grogan 1997). The Elasmobranchii contains three infraclasses: †Cladoselachimorphi, †Xenacanthimorpha, and Euselachii. Euselachii is the only infraclass with extant species (Nelson 2006 and references cited therein). Within Euselachii, two conflicting phylogenetic hypotheses exist. The first (outlined by Nelson 2006), coined the hypnosqualean hypothesis, places the batoids (Rays) as sister to the Pristiophoriformes (Saw Sharks) and the two are sister to Squantiformes (Angel Sharks), all ultimately sharing a common ancestor with Squaliformes (Dogfish Sharks) (see morphological works by de Carvalho 1996; Shirai 1996). The second hypothesis, summarized in and accepted by

Table 4.1. Life history information for the genus *Dasyatis* compiled from numerous sources but mostly for *Dasyatis sabina* (see text for citations; DW = disc width).

Number of extant species	About 38
1 or 2 degree freshwater	2
Maximum size recorded in length	Females, 37 cm DW; males, 32.6 cm DW
Maximum age	About 9 years
Age and size at first reproduction	Probably age 1+; females, 22–24 cm DW; males, 20.5–25.0 cm DW
Iteroparous or semelparous	Iteroparous
Fecundity estimates	2.3 young/female
Egg deposition sites	Ovoviviparous
Clutch size	Not applicable
Range of nesting and spawning dates and temperatures	Fertilization occurs between early March and mid-April at about 25°C, but mating can be protracted (August to mid-April)
Habitat of spawning sites; average water depth	Similar to general habitat
Incubation period; larval type at hatching	About 3.5–4 months from fertilization to parturition; ovoviviparous so larval type not applicable
Mean size at hatching	96.5 ± 8.0 mm DW
Parental care	Female carries embryos until parturition (about late July)
Major dietary items	Small benthic crustaceans, polychaete worms, and other small invertebrates
General year-round habitat	1–2 m deep water; soft, mud bottom mixed slightly with sand toward the littoral zone
Migratory or diadromous	Little migration known in the freshwater populations
Imperilment status	Currently stable over historic range

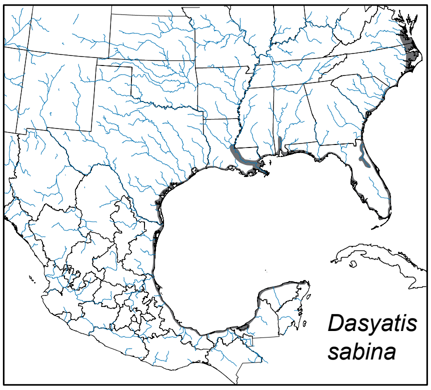

Figure 4.1. Geographic range of the Atlantic Stingray, *Dasyatis sabina*, in North America.

Nelson (2006) and used here, is coined the selachian-batoid hypothesis, which considers Squaliformes monophyletic without inclusion of the batoids (see Schwartz & Maddock 2002; Douady et al. 2003; Maisey et al. 2004; Naylor et al. 2005).

Relationships within Dasyatidae

Of the six genera within the dasyatids, Lovejoy (1996) and McEachran et al. (1996) placed the genera *Taeniura* and amphi-American *Himantura* within the potamotrygonid clade; however, Nelson (2006) placed them within the dasyatid clade, as is done here. *Pteroplatytrygon violacea* is sometimes placed in *Dasyatis* (Nishidia 1990; Lovejoy 1996; Rosenberger 2001b; see also Compagno 1999b), which would render it the only known species of *Dasyatis* to be mostly pelagic and to solely use an oscillatory-based pectoral motion. Other species of *Dasyatis* use an undulatory-based pectoral motion (Rosenberger 2001a) (see morphology section).

To date, no synapomorphies are known that unite species within *Dasyatis* or species within *Himantura* (Lovejoy 1996; McEachran 1996; Rosenberger 2001b). Thus, both genera are either paraphyletic or polyphyletic. The phylogenetic relationships of *Dasyatis* to other genera or of some species within the genus (see the following subsection) are uncertain. Traditionally, the genera were separated by the use of one character—the presence or absence of tail fin folds (folds occur in *Dasyatis* and are absent in *Himantura*, Bigelow & Schroeder 1953a). Resolution of the dasyatid clade would help elucidate evolutionary relationships across the myliobatids (de Carvalho et al. 2004).

Interspecific Relationships

Using morphological characters in a parsimony analysis, Rosenberger (2001b) analyzed species relationships for

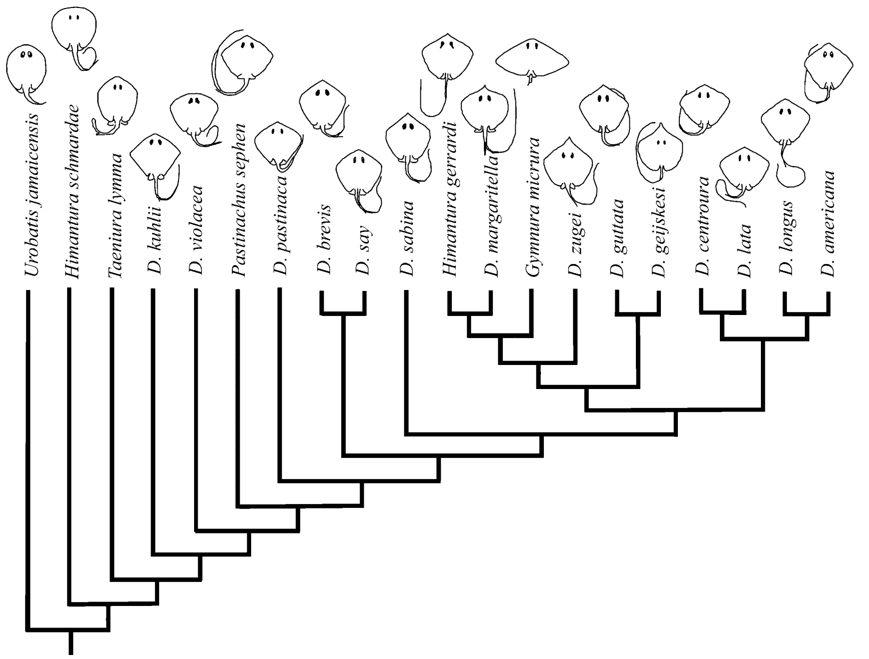

Figure 4.2. Partial phylogeny of the family Dasyatidae containing 20 species, including the Atlantic Stingray, *Dasyatis sabina* (redrawn from Rosenberger 2001b).

14 of 35 species within *Dasyatis* and found several sister-species pairs (Fig. 4.2). *Dasyatis sabina* was basal to a large clade of eight other species of *Dasyatis* and the genera *Himantura* and *Gymnura*. From this work, the genus *Dasyatis* is not monophyletic (see also Nishidia 1990; Lovejoy 1996; McEachran et al. 1996).

FOSSIL RECORD

The Myliobatiformes have a diverse and widespread fossil record that spans both freshwater and marine habitats, but most of the fossil specimens are incomplete and consist of only individual teeth, dermal denticles, and serrated caudal spines (de Carvalho et al. 2004). Fossil records span five geological epochs (55.5–2.6 mya): the Paleocene, Eocene, Oligocene, Miocene, and Pliocene (see compilation by de Carvalho et al. 2004). Presently, more complete fossils are known from only two localities, each representing different paleoenvironments: Monte Bolca Formation, northeastern Italy, and the Green River Formation, Wyoming. The Monte Bolca Formation was a tropical marine reef (de Carvalho et al. 2004) and the Green River Formation a collection of tropical to subtropical lakes. Both localities are Eocene (55.8–33.9 mya) in age (Grande 1984, 2001).

The fossil record within Dasyatidae is complex and subject to debate about phylogenetic position of extant species or if the family should be assimilated into the Potamotrygonidae. †*Heliobatis radians*, described from Fossil Butte (Eocene, 55.8–33.9 mya) of the Green River Formation, has been placed in Dasyatidae (Grande 1984) and Heliobatidae (de Carvalho et al. 2004). Synonyms of †*Heliobatis* include †*Xiphotrygon acutidens* and †*Palaeodasybatis* (de Carvalho et al. 2004). One other genus is based on incomplete fossil material and is subject to reinterpretation in the future. The genus †*Coupatezia* occurs from the Middle Eocene (48.6–37.2 mya) of Africa, Europe, and North America and was placed provisionally within Dasyatidae based on tooth structure. North American records include †*C. woutersi* from Chesapeake sediments (Eocene, 55.8–33.9 mya) (Ward & Weist 1990), †*C. woutersi* specimens from Lauderdale County, Mississippi (Early Eocene, 55.8–48.6 mya) (Case 1994), and †*C. woutersi* from Virginia (Early Eocene, 55.8–48.6 mya) (Kent 1999). No fossil records are specifically attributable to *Dasyatis sabina*.

MORPHOLOGY

Stingrays are cartilaginous, dorsally flattened fishes, the flattened portion of the body being referred to as the disc (Figs. 4.3 and 4.4). The gill openings and mouth (with usually protrusible jaws) are on the ventral surface of the body. The pectoral fins are expanded laterally, becoming thin toward the outer edges to form wing-like structures that attach to the body in front of the gills on the sides of

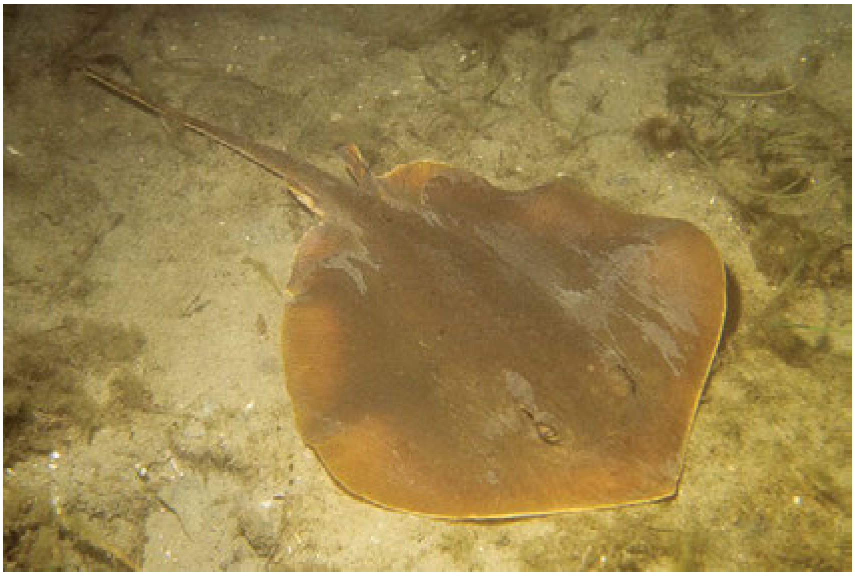

Figure 4.3. A single individual male of the Atlantic Stingray, *Dasyatis sabina*, from Jupiter, Florida (photo courtesy of, copyrighted by, and used with permission of David B. Snyder).

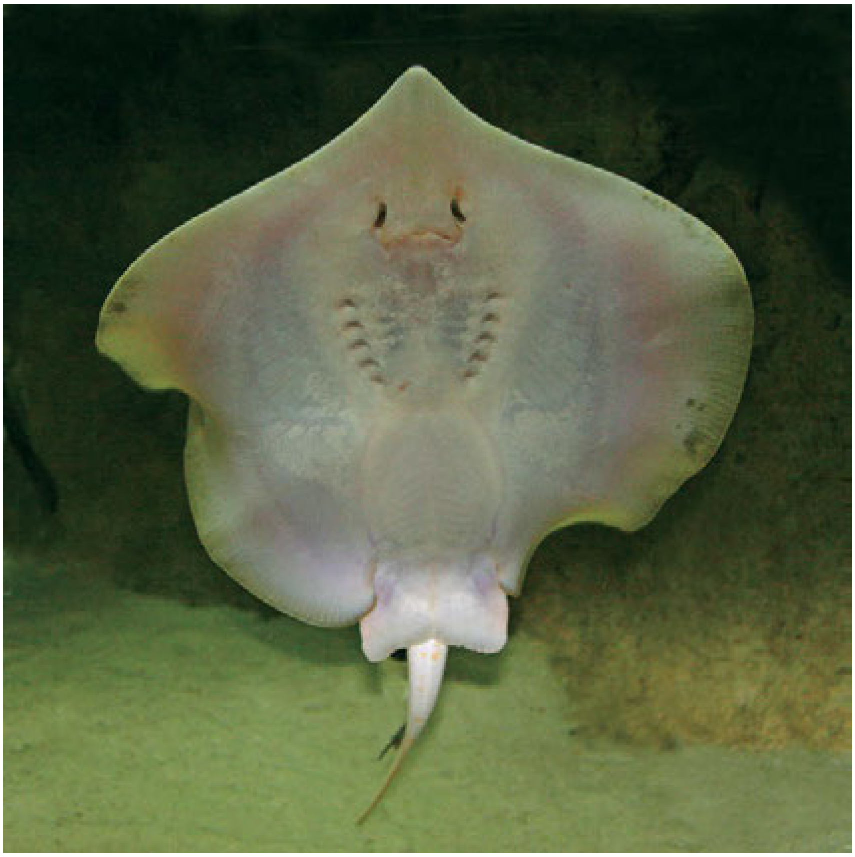

Figure 4.4. Ventral view of a female Atlantic Stingray, *Dasyatis sabina*, in the Mote Aquarium, Sarasota, Florida (photo courtesy of, copyrighted by, and used with permission of Larry Linton).

the head. The pelvic fins are expanded laterally with a convex lateral margin that is partially overlapped by the pectoral fins. The eyes and spiracles are located dorsally with the anterior portion of the head not elevating from the disc. The dorsal fin is absent, and the caudal fin tapers into a filament. The anterior vertebra is fused to form a synarcual with the suprascapular of the pectoral girdles joined dorsally; the vertebral column is fused with the synarcual.

All Whiptail Stingrays have a disc shape that is <1.3 times wider than long and is thin and slender with an oval to trapezoidal appearance. They lack a caudal fin. The tail is long and slender (distance from cloaca to tip of tail greater than width of disc) and is distinctly demarcated from the disc. The tail has one or more long, serrated venomous spines situated along the medial half of the dorsal surface. A few species have longitudinal tail folds (fin folds) on the upper or lower surface. The pelvic fins are expanded variably, ranging from blunt to pointed. The snout is usually obtuse or rounded, occasionally pointed. The floor of the ventrally located mouth has fleshy papillae and usually 28–36 bands of blunt teeth along the jaws (conical in breeding males). The body is naked, but some species possess small to medium-sized tubercles on the dorsal surface of the disc and tail. The dorsal surface of the body is usually gray to dark brown, sometimes with dark or pale markings; the ventral surface of the body is generally whitish. Maximum disc width is 210 cm (in *Dasyatis centroura*, Roughtail Stingray) but less than half that in most species.

The Atlantic Stingray has a triangular snout at the apex of the body disc; the snout length anterior to the orbits is considerably longer than the distance between the spiracles. The disc has broadly rounded corners and is relatively smooth except for a linear row of 12–15 hard tubercles running linearly down the midline of the back, but the tubercles are absent on the tail beyond the pelvic fins (Robins & Ray 1986). A well-developed, longitudinal cutaneous fold runs along both the upper and lower surfaces of the tail. The upper surface of the body is a yellowish-brown to brown color with a paler pigment pattern toward the margin of the disc; the ventral portion of the disc is white in small- to medium-sized individuals, sometimes margined with gray-black in larger specimens. The head is slightly elevated with the disc size being about 1.1 times wider than long. Sexual dimorphism occurs in size, the male intromittent organ, and dentition (see reproduction section).

Reproductive Morphology

The testes of the Atlantic Stingray are paired structures that are dorsoventrally flattened and suspended from the dorsal wall in the anterior peritoneal cavity. Each testis is fully functional with the right testis being reduced in size. Each testis is composed of lobes that project inward from the gonad surface with each lobe containing spermatocysts in various stages of spermatogenesis. The mature sperm passes through the collecting ducts, the vas efferens, the vas deferens, and the Leydig's gland to its eventual storage location, the seminal vesicles (Maruska et al. 1996).

The ovaries, like the testes, are paired and suspended from the peritoneal cavity. Only the left ovary is functional, producing visible ova; the right ovary is reduced in size. The ovaries of mature individuals contain oocytes throughout the year that are embedded in the connective tissue; the onset of ova maturation (October–November) marks the growth and development of the oocytes. During ovulation (March–April) the largest mature ova are released from the ovary, moving to the ostium and oviduct. The remaining mature ova migrate to the external ovarian surface (Maruska et al. 1996).

Maximum Size

Dasyatis sabina is the smallest species of Stingray in the Western Atlantic Ocean. Size of Rays is expressed typically as disc width (DW) rather than the more conventional body length. In a North Carolina sample (Schwartz & Dahlberg 1978), 25 individuals were >380 mm DW with the largest males and females measuring 460 mm and 490 mm DW, respectively. The largest female weighed 5,433 g. Individuals from a Georgia sample had smaller maximum sizes (292 mm DW for males and 405 mm DW for females). Males and females along the Florida east coast and in the St. Johns River typically are smaller (≤300 mm and ≤400 mm DW, respectively) and show bimodal size distributions (Snelson et al. 1988; Johnson & Snelson 1996). The apparent bimodal size distributions of Florida and North Carolina populations, which may have been an artifact of sampling or based partly on misidentifications, likely were more attributable to differences in age, growth, and mortality characteristics of the respective populations (Snelson et al. 1988; Johnson & Snelson 1996). The larger size of the North Carolina samples led Snelson et al. (1988) to suggest the possibility that the North Carolina population is distinctly larger bodied or that size data are confused by misidentifications. A report of four specimens with disc widths (DW) ranging from 458 to 610 mm (Fowler 1926) was questioned as being too large and was almost certainly based on misidentified individuals (Lewis 1982; Snelson et al. 1988).

Spine Morphology and Replacement

Stingray tail spines are composed of an inner core of vasodentine and a thin outer layer of enamel-like material (Halstead et al. 1955). Spines have retrorse serrations along the lateral margins, a sharp tip, longitudinal grooves on both the dorsal and ventral surfaces, and a raised longitudinal ridge along the ventral surface. The spines are covered by integumentary and glandular tissues. Venom is produced in the tissues covering the spine (Halstead et al. 1955; Haddad et al. 2004; Barbaro et al. 2007). The venom of *Dasyatis* spp., although apparently not as toxic as that of Neotropical freshwater *Potamotrygon* spp., nevertheless induces severe pain and depending on the dose may cause shortness of breath, agitation, convulsion, and swelling in victims (Barbaro et al. 2007).

Spines are replaced periodically with many individuals in summer in both freshwater and marine populations having two spines. In late May or June an incipient secondary (replacement) spine becomes visible just posterior and ventral to the existing primary spine (Teaf & Lewis 1987; Amesbury & Snelson 1997). Replacement is rapid and synchronous with the mean spine count / individual increasing from one to two over a period of 3 weeks. Nearly all individuals exhibit two spines until early August when specimens with only a single spine become increasingly prevalent. At that time, individuals with a single spine often have a small white scar on the dorsal surface of the tail just anterior to the base of the existing spine, indicating the recent loss of the primary spine, rendering the secondary spine as the new primary spine.

Type of Locomotion

Batoid fishes primarily propel themselves in two different ways: pectoral fin–based locomotion or axial-based locomotion (body and tail). Pectoral fin–based locomotion is of two types: undulation and oscillation. Undulation, or rajiform locomotion, occurs when >1 wave is present on the fins at a time; oscillation of the pectoral fins, or mobuliform locomotion, occurs when the fins move up and down with less than half a wave on each fin. The Atlantic Stingray, like most benthic Rays, moves through undulation (Rosenberger 2001a; Table 4.2). They also exhibit an augmented form of pelvic fin punting, or benthic walking, in which the pectoral fins are also undulated as the anterior lobe of each pelvic fin synchronously is protracted cranially, placed into the substrate, and retracted caudally, creating a forward thrust (Macesic & Kajiura 2010).

Morphology and Mechanosensory Function of the Lateral-Line System

The lateral-line system in fishes is used to detect water movements relative to the organism's body surface

Table 4.2. Summary of swimming kinematics for the Atlantic Stingray, *Dasyatis sabina* (data from Rosenberger 2001).

	Range			
Variable	**Minimum**	**Maximum**	**Mean**	**Standard Deviation (SD)**
Fin-beat frequency (Hz)	1.91	3.41	2.51	0.36
Mid-disc amplitude (proportion of disc width)	0.09	0.2	0.15	0.03
Wavespeed (proportion of disc length)	1.65	3.46	2.59	0.46
Wave number	1.08	1.56	1.31	0.12
Stride length (cm)	53.33	221.59	104.9	33.71
Phase velocity	0.46	0.97	0.76	0.13

Table 4.3. Summary of morphological features of the lateral-line system in the Atlantic Stingray, *Dasyatis sabina* (data from Maruska 2001).

Surface	**Dorsal**	**Ventral**
SN location (number)	Bilateral medial rows to end of tail (about 100/side)	None
VS location (number)	None	Bilateral rows along rostrum midline (6–10/row)
Pored canals	HYO, IO, SO, PLL	HYO, MAN (SPL present)
Number of pores/tubule canals	1	1–20
Non-pored canals	HYO, IO, SO	IO, HYO

HYO=hydromandibular, IO=infraorbital, MAN=mandibular, SO=supraorbital, SPL=subpleural loop, SN=superficial neuromast, VS=vesicles of Savi.

(Kalmijn 1989; Coombs 1994; Coombs et al. 1996); the functional units of the lateral-line system are neuromasts, which are mechanosensory hair cells and gelatinous support cells (Maruska & Tricas 1998; Maruska 2001). Elasmobranch fishes, including Stingrays, have several types of mechanosensory lateral-line organs that are morphologically and functionally distinct. Three types of neuromasts exist: the superficial neuromast, or pit organ, which is located on the skin surface with the cupula exposed to the water; the canal neuromasts, which are located in dermal or subdermal canals and make contact with water through pores on the surface of the skin; and the vesicles of Savi, which are mechanoreceptors found in subdermal pouches on the ventral surface (these are only found in some torpediniforms, Electric Rays, and dasyatids). The skin surface of the Atlantic Stingray contains superficial neuromasts, and canal neuromasts occur in the subdermal canals, the hyomandibular, infraorbital, supraorbital, posterior lateral line, and mandibular canals. The vesicles of Savi are located on the isolated subdermal pouches on the ventral surface of the rostrum (Table 4.3; Fig. 4.5) (Maruska & Tricas 1998; Maruska 2001).

Little is actually known of the function of these systems, but superficial neuromasts appear best positioned to detect water movements along the transverse body axis (e.g., detecting movements produced by tidal currents, conspecifics, or predators) (Maruska & Tricas 1998; Maruska 2001). The pored, dorsal-canal system may detect water movements created by conspecifics, predators, or flow field distortions during swimming. Morphological examination of this system in the Atlantic Stingray led to the mechanotactile hypothesis, which contends that the ventral, nonpored canals and vesicles of Savi function as specialized tactile mechanoreceptors that help in detection and capture of small benthic invertebrate prey (Maruska & Tricas 1998).

Vision

The Atlantic Stingray, like other studied elasmobranchs, exhibits a variety of advanced visual features such as mobile pupils, multiple visual pigments, visual streaks, and a moveable lens. The species possesses a ramp retina (Sivak 1975) that permits simultaneous focus of images at various distances (McComb & Kijiura 2008) and rods and cones (requisite for color vision). Cones decrease in density peripherally on the retina, but the species has a cone-rich band located along the horizontal axis of the retina,

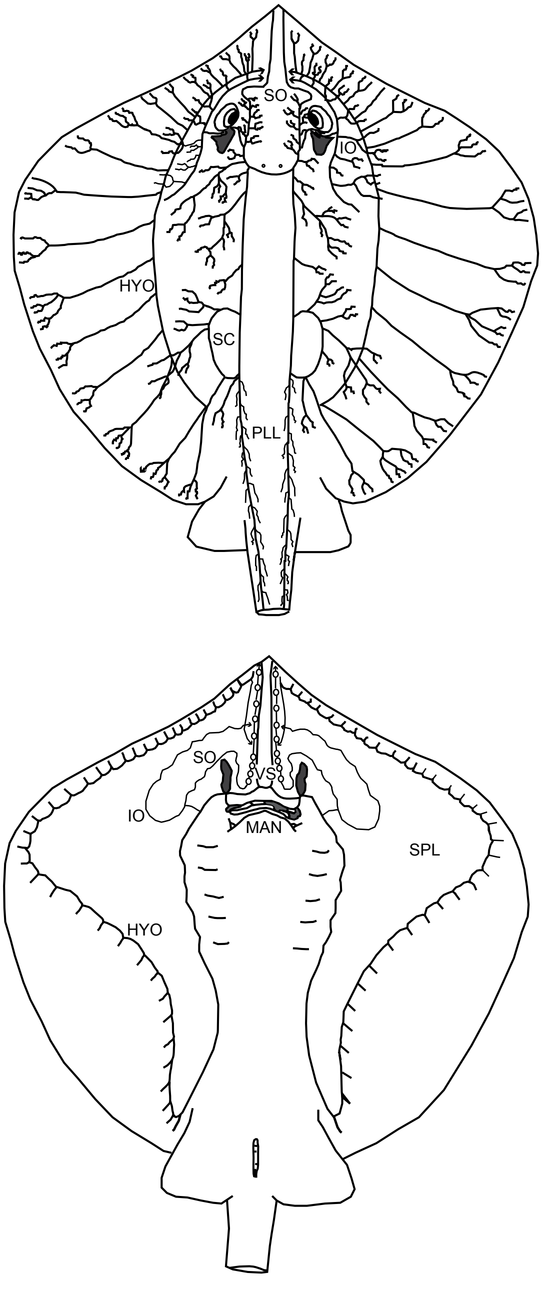

Figure 4.5. Distribution of the lateral-line canal system and vesicles of Savi on the dorsal (*top*) and ventral (*bottom*) surface of the Atlantic Stingray, *Dasyatis sabina*. Dorsal canals contain numerous lateral tubules that terminate in pores across the body surface. The infraorbital, supraorbital, and sections of the hyomandibular canal near the mouth and rostrum and along the ventral midline lack pores but do contain innervated neuromasts. Vesicles of Savi are located in bilateral rows on the ventral rostrum midline and are isolated from the surrounding water, but lumina of adjacent vesicles are connected via tubules. HYO = hyomandibular canal, IO = infraorbital canal, MAN = mandibular canal, PLL = posterior lateral-line canal, SC = scapular canal, SO = supraorbital canal, SPL = subpleural loop, VS = vesicles of Savi (redrawn from Maruska 2001).

termed a horizontal visual streak, which likely enhances visual acuity within the horizontal monocular visual field (Logiudice & Laird 1994) (see physiology section). Atlantic Stingrays commonly partially bury themselves in the substrate, in part as a mechanism of predator avoidance. When the individual is buried, however, the eyes remain exposed. The visual streak might allow the individual to scan the horizon for predators (e.g., Sharks) without the revealing head and eye movements necessary in animals with a fovea (Logiudice & Laird 1994).

GENETICS

The genetics of the Atlantic Stingray are little studied. The species is being used in molecular and functional characterization studies (e.g., urea transporters, Janech et al. 2006ab) and in comparative studies of genes and enzyme products such as those regulating important steroid hormones and those involved in acid-base and ion regulation.

Karyology

In a sample of 10 Atlantic Stingrays from the Texas coast, the diploid (2n) chromosome count was 68; a congener, the Bluntnose Ray (*Dasyatis say*), also had a count of 68 (Donahue 1974). In the Atlantic Stingray, 28 chromosomes had median to submedian centromeres, and 40 had subterminal to terminal centromeres. Within the median-submedian group, 20 were large and 8 were relatively small. In the subterminal-terminal group, only the largest pair was clearly distinguishable as homologous. Male heterogamety was suggested by a pair in the median-submedian group, but the size distinction varied among the seven males examined.

Comparative Genomics

The sequence of the cytochrome P450 aromatase (P450arom) of the Atlantic Stingray was characterized to provide insights into the evolution of this steroidogenic cytochrome (Ijiri et al. 2000). The P450arom enzyme mediates the conversion of androgens (i.e., testosterone and androstenedione) to estrogen and is a key enzyme in the steroidogenic pathway. Hence, in vertebrates it plays an important role in the onset of sexual maturity, development of gametes, expression of sexually dimorphic characters, and evoking of reproductive behaviors. With comparative data from mammals, birds, reptiles, and teleosts, the phylogenetic relationship (neighbor-joining method, Kimurua protein distances) of the Atlantic Stingray P450arom suggested it as a unique evolutionary lineage having a common ancestral root with both the higher vertebrates and teleosts. Interestingly, especially given the relatively ancient origin of the elasmobranchs, including the Stingrays, the P450arom of the Atlantic Stingray was 56–59% identical to avian and mammalian forms of P450arom and 53–57% identical to that of bony fishes.

In a physiologically oriented study using genetic techniques, the Atlantic Stingray yielded the first full-length H^+-K^+-ATPase (HKα1) transcript for any fish (Choe et al. 2004). The H^+-K^+-ATPases participate in systemic ion and acid-base regulation in animal stomachs, including that of the Atlantic Stingray (e.g., Smolka et al. 1994), but also are associated with similar functions in mammalian kidneys. Many of the functions of the mammalian kidney are accomplished by the gills in elasmobranchs. The reported similarities between mammalian type B intercalated cells in the cortical collecting duct of the mammalian kidney and elasmobranch epithelial cells (Piermarini et al. 2002) led to work revealing that HKα1 was expressed in the gills of the Atlantic Stingray (Choe et al. 2004). Within the gills, HKα1 expression did not increase under conditions of hypercapnia (increased carbon dioxide in the blood) but was increased in fresh water, suggesting an active role in osmoregulation via potassium transport. A phylogenetic analysis (rooted tree, ClustalV alignment) of the putative Atlantic Stingray HKα1 with available full-length HKα1 sequences (frog, rat, pig, rabbit) placed the Atlantic Stingray HKα1 as basal to the other taxa. This dates the origin of the H^+-K^+-ATPases to at least before the division of bony and cartilaginous fishes (Choe et al. 2004).

PHYSIOLOGY

Several aspects of Atlantic Stingray physiology are documented. Studies examined urea biochemistry in muscle tissue (Treberg et al. 2006); interaction effects of osmoloytes on calcium binding (Heffron & Moerland 2008); ion transport in gills (Piermarini & Evans 2001; Piermarini et al. 2002) and the alkaline gland (Grabowski et al. 1999); the role of the inter-renal gland in glucocorticoid and mineralocorticoid systems (Andrews et al. 2010); electro-olfactogram responses to amino acids (Silver 1979; Meredith & Kajiura 2010); reproductive histology and endocrinology (Maruska et al.

1996; Büllesbach et al. 1997; Snelson et al. 1997; Volkoff et al. 1999; Forlano et al. 2000; Tricas et al. 2000; Piercy et al. 2003; see reproduction section); and biochemical, structural, and comparative neurology (Rosiles & Leonard 1980; Ritchie & Leonard 1983; Ritchie et al. 1984; Livingston & Leonard 1990; Bernau et al. 1991; Puzdrowski & Leonard 1993, 1994; Nunez & Trant 1999; Puzdrowski & Gruber 2009). The focus here is on metabolism, osmoregulation and salinity tolerance, sensitivity to conductivity, temperature tolerance, the visual field, and electroreception. Little else appears to be available on other environmental tolerances (e.g., pH, dissolved oxygen, turbidity).

Metabolism

Metabolism of marine elasmobranch fishes differs slightly from that of bony fishes because of a low capacity for extra-hepatic lipid oxidation, and thus an increased reliance on ketone bodies as the substrates for oxidation. This is most likely a consequence of the osmotic strategy (the retention of high levels of urea and methylamines in the tissues) because the urea disrupts the hydrophobic interactions that are necessary for the proper structure and function of proteins. The transport of fatty acids is dependent on binding to albumin; hydrophobic interactions mediate the binding of fatty acids to albumin, thus the increase in urea concentrations most likely led to the evolution of ketone body– and amino acid–based extra-hepatic metabolic organization instead of the fatty acid system seen in the bony fishes. In addition, within *Himantura signifer* (White-edged Freshwater Whip Ray), a negative relationship was seen in liver glutamate dehydrogenase activity and tissue and plasma urea levels, indicating that glutamate is deaminated in freshwater elasmobranchs because of the different levels of tissue and plasma urea seen in these species (Speers-Roesch et al. 2006).

Osmoregulation and Salinity Tolerance

Chondrichthyan fishes are well adapted for living in a marine environment, a consequence of their unique ability to actively conserve urea and trimethylamine oxide (nitrogenous end products) in the blood and tissues. These organic solutes are freely filterable through the kidney and are actively reabsorbed by the renal tubules (Janech et al. 2003). Their subsequent accumulation in body fluids and tissues lowers the diffusion pressure of water such that it can be drawn into the animal from the surrounding environment without the expenditure of free energy. Considering this unique adaptation, it follows that nearly all known species of chondrichthyans live exclusively in salt water.

Organisms in fresh water must obtain ions from the environment through active branchial uptake to maintain hyperosmolarity of tissues relative to the surrounding environment; ions also are gained from the esophagus and intestines (Perry 1997). Within fresh water, euryhaline elasmobranchs maintain high concentrations of urea in plasma, around 100–250 mmol/l, and the Atlantic Stingray has substantially higher sodium, chloride, and urea concentration (almost double) compared with freshwater teleosts (Piermarini & Evans 1998). Early tests of acclimation to dilute seawater indicated Atlantic Stingrays are efficient regulators of osmolarity and may be better adapted to maintaining high plasma osmolarity than Sharks (De Vlaming & Sage 1973). When transferred to dilute sea water, body weight increased and hematocrit decreased but returned to normal within 6 days. Further, physiological studies measuring the ability of Atlantic Stingrays to regulate body fluids revealed a remarkable kidney (glomerular and tubular) functional reserve that allows the species to produce copious amounts of solute-free urine in fresh or low-salinity water (Janech & Piermarini 2002; Choe & Evans 2003; Janech et al. 2006a). Urine flow rate of Atlantic Stingrays in dilute sea water was nine times higher than that of individuals maintained in sea water. The glomerular filtration rate in dilute sea water is among the highest reported for any elasmobranch. This ability results in little increase in weight and little change in hematocrit values in fresh water.

The Atlantic Stingray shows no difference in salinity tolerances between the freshwater and marine populations and even the freshwater population has not lost the ability to osmoregulate in salt water as have the Neotropical freshwater species in South America. A molecular and functional comparison of calcium-binding proteins (parvalbumins) in the presence of osmolytes, including urea, revealed no differences between Atlantic Stingrays from marine water and those from fresh water (Heffron & Moerland 2008). In the population of *D. sabina* in the upper St. Johns River, Florida, the gills are important for active ion uptake in fresh water, but the rectal gland is important for active sodium chloride excretion in sea water (Piermarini & Evans 1998, 2000). As such, the weight of the salt-secreting rectal gland in the freshwater population is <80% that in the marine counterpart (Piermarini & Evans 1998).

Even in marine populations the Atlantic Stingray can occupy a broad range of salinities. In fact, throughout its range the Atlantic Stingray has been recorded numerous times from low-salinity waters (0.2–1.0 ppt), occurrences that generally are limited to warmer months of the year (Schwartz & Dahlberg 1978). Such occurrences are from South Carolina (Bearden 1965); the St. Lucie and Caloosahatchee Rivers, Florida (Gunter & Hall 1963, 1965); the Florida Everglades (Loftus & Kushlan 1987); and the Mississippi Sound and Atchafalaya Bay, Mississippi and Louisiana (Funicelli 1975; Juneau 1975). In North Carolina, individuals occupy a salinity range of 0–35 ppt (Schwartz 1995, 2000). Similarly, in a Florida estuary the species was captured at salinities ranging from 15 to 41 ppt (Snelson & Williams 1981; Snelson et al. 1988). These records are from areas subject to tidal influence in which the water may vary from fresh to brackish depending on time of day and associated tidal conditions. The situation also is complicated in that the precise part of the water column where salinities are recorded is rarely indicated. Since salt water is more dense (i.e., heavier) than fresh water, and since Stingrays live on or near the bottom, this can be an important consideration. Swift et al.'s (1977) intensive fish survey of the Ochlockonee River, Florida, which included records from 100 different stations throughout the drainage (some sampled multiple times), is one of the few studies in which precise data of this nature were provided. There *Dasyatis sabina* occurred only at the seven most downriver stations with the lowest recorded bottom salinity of 2.5 ppt.

The principal region of occurrence of the Atlantic Stingray in permanent fresh water, well upstream of tidal influence, and the source of the vast majority of confirmed records, is the St. Johns River, Florida, with records from Lake Monroe, near Sanford, dating back more than a century (Bean 1884). The species has since been observed many times throughout the river (McLane 1955), upstream at least to Lake Jesup, about 300 km upstream of the river's mouth (Johnson & Snelson 1996; Piermarini & Evans 1998, 2000). Maximum upriver tidal influence in the St. Johns varies, but in general, any fish recorded from Lake George is considered to be from fresh water (Johnson & Snelson 1996). The northern end (the mouth) of Lake George is >160 km from the Atlantic Ocean. The St. Johns River is unique among major North American rivers in that it originally was a marine embayment bordering the northeast Florida coast, which was partially isolated by a series of offshore barrier islands. Gradually these islands became coalesced to create the St. Johns River as it exists today. The river is fed by many freshwater streams, entering mostly from the west, together with numerous springs of varying chemical composition, ranging from fresh to slightly saline (Upchurch & Randazzo 1997). Invasion of marine species into low-salinity waters in Florida was possible due to the presence of Pleistocene salt deposits that contribute to increased chloride levels in otherwise freshwater systems (Odum 1953). The complex water chemistry of the river, which is related to its unique origin and chemical composition of the underlying strata, means that pockets of brackish water are scattered throughout the drainage, which in turn has resulted in a fish fauna that is unique in its mixture of freshwater and marine species. Some of the marine species are rarely if ever encountered elsewhere in riverine environments. In addition to *Dasyatis sabina*, this includes marine teleost fishes such as *Elops saurus* (Ladyfish), *Opisthonema oglinum* (Atlantic Thread Herring), *Mugil curema* (White Mullet), *Membras martinica* (Rough Silverside), *Syngnathus scovelli* (Gulf Pipefish), *Eucinostomus harengulus* (Tidewater Mojarra), *Micropogonias undulatus* (Atlantic Croaker), *Lutjanus griseus* (Gray Snapper), *Microgobius gulosus* (Clown Goby), *Gobiosoma bosc* (Naked Goby), and *Paralichthys lethostigma* (Southern Flounder).

Other freshwater records for *Dasyatis sabina* from localities well beyond tidal influence are from the Mississippi River in Louisiana and the Tombigbee River in Alabama. Gunter (1938) reported the Atlantic Stingray from the Mississippi River at New Orleans and Angola, Louisiana, the latter >322 km upstream of the river's mouth. He also noted that Stingrays are occasionally caught during the summer months in the Atchafalaya River at Simmesport, Louisiana, >257 km upstream from the mouth. Boschung & Mayden (2004) reported the species from the Tombigbee River (Mobile Bay basin) upstream as far as Jackson, Clarke County, Alabama. Unlike the St. Johns River, freshwater reproduction for this species is not confirmed in either the Mississippi River or Mobile Bay basins, although this seems likely in the Mississippi River considering the distance this species has been found upstream. The source of a record for *D. sabina* from the Chattahoochee River (Apalachicola River drainage) in the extreme southeastern corner of Alabama is uncertain (see Ross & Burgess 1980; Boschung & Mayden 2004). No voucher specimens from this locality or elsewhere in the Apalachicola River drainage apparently exist, and none of the above authors can recall the basis for this record.

Sensitivity to Low Conductivity

Indirect evidence suggests the freshwater population of Atlantic Stingrays in St. Johns River, Florida, can be affected negatively by low water conductivity (<700 µMhos/cm). A large-scale die-off of numerous individuals of all sizes and both sexes occurred between September and December 1991 in Indian River Lagoon, which coincided with a 7-month period of extremely low water conductivity for the region. Whether this reflected direct osmotic stress or loss of important food resources is unclear (Johnson & Snelson 1996).

Temperature Tolerance

Across their broad latitudinal range in shallow continental waters (New England to Mexico), some populations of Atlantic Stingrays experience seasonal water temperature changes of ≤35°C and daily shifts of ≤10°C. Unsurprisingly, Atlantic Stingrays are one of the most thermally tolerant fish known, enduring temperatures between 0.4 and 43°C (Bigelow & Schroeder 1953a; Snelson et al. 1988; Fangue & Bennett 2003). Their innate thermal tolerance zone also is large, allowing them to exploit a wide temperature range regardless of previous thermal acclimation history (Fangue & Bennett 2003). Using an endpoint of spiracle cessation for 1 min and laboratory acclimation temperatures of 10.8, 20.5, or 35.1°C, the critical thermal maxima for the species were 35.7, 39.3, and 43.2°C, and the critical thermal minima were 0.8, 4.8, and 10.8°C, respectively. When exposed to diel thermoperiods of 34.0–37.3°C and 7.0–11.0°C, Atlantic Stingrays had critical thermal maxima of 43.1 and 33.4°C and minima of 9.6 and 0.3°C, respectively. The thermal tolerance polygon, estimating the species' entire thermal tolerance niche, was 978°C^2, which is one of the largest ever measured in a fish (Fangue & Bennett 2003). Interestingly, the intrinsic thermal acclimation zone, the tolerance independent of previous thermal history, was 692°C^2, accounting for about 71% of the overall thermal niche.

In the wild, the species seems particularly sensitive to cold but not warm water temperatures. In coastal lagoons of Florida, the species was not present in shallows in winter unless water temperatures were >16–18°C. The species occurred, however, in waters as warm as 35°C, and individuals did not leave shallow water in mid-summer when afternoon temperatures were regularly >30°C (Snelson et al. 1988).

Thermal preference in Atlantic Stingrays is affected by parturition and feeding. When acclimated at 29°C, males, pregnant females, and non-pregnant females all preferred temperatures lower than the acclimation temperature but well within the summer thermal milieu experienced in the wild (Fangue & Bennett 2003). Males and pregnant females showed highest preferred temperatures of 26.1 and 25.9°C, respectively, which were not statistically distinguishable. Non-pregnant females preferred a slightly lower and statistically different average median temperature of 25.3°C. The preference of pregnant females for higher temperatures, even though seemingly slight, may increase embryonic growth rate and decrease the gestation period. A 1°C difference could reduce gestation time by ≥14 days. After feeding, females (pregnant and non-pregnant), but not males, selected lower temperatures. Although the mechanism is hypothetical and not entirely clear, migration to cooler waters after feeding might increase food absorption rates relative to evacuation rates and result in an energetic benefit (Wallman & Bennett 2006). Clearly, however, Atlantic Stingray movement and distribution are a function, at least in part, of the physiological effects of temperature.

Visual Field

In an assessment of the visual field among four batoids, the Atlantic Stingray was characterized as having Type III vision (McComb & Kajiura 2008). The Type III visual field is characteristic of predators with large eyes that show a reduction in vigilance behavior. Visual fields were measured in three ways: the field of view of a single eye (monocular), the combined field of view of both eyes (cyclopean), and the overlap of the monocular fields (binocular) (Fig. 4.6). The point at which the monocular visual fields overlap is termed the "binocular convergence point," and the distance from this point to the central point between

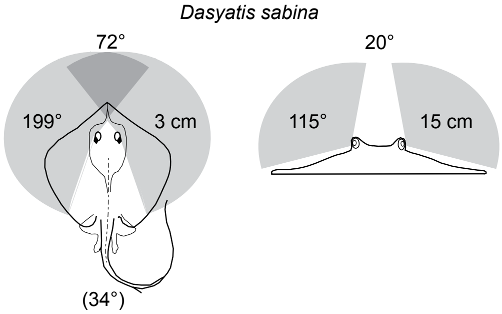

Figure 4.6. The static functional horizontal and vertical visual fields of the Atlantic Stingray, *Dasyatis sabina*. Values within the shaded area represent monocular visual fields (*left*) and the standardized convergence distance (*right*). Values shown outside the shaded areas represent binocular overlaps, and values in parentheses indicate blind areas (redrawn from McComb & Kajiura 2008).

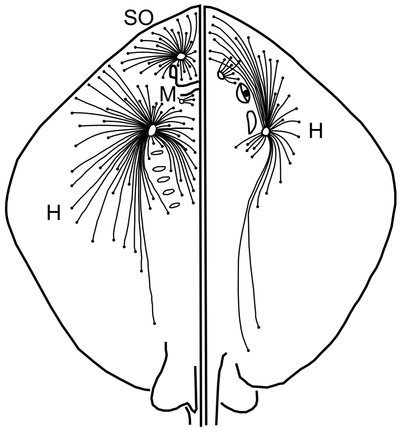

Figure 4.7. Distribution of the electrosensory canals of the ampullae of Lorenzini over the ventral (*left*) and dorsal (*right*) surfaces of the Atlantic Stingray, *Dasyatis sabina*. H = hyoid cluster group; M = mandibular cluster group; SO = superficial ophthalmic cluster group (redrawn from Sisneros & Tricas 2000 with permission of Timothy C. Tricas, University of Hawaii at Manoa).

the eyes (in the transverse plane) is called the "convergence distance." A relatively short convergence distance provides depth perception beginning closer to the eyes, but a longer convergence distance conveys binocular vision farther from the eyes. Type III visual fields consist of broad binocular overlaps (~50 degrees) that are coupled with large posterior blind areas and are seen in fast-moving predators that may simultaneously use other sensory modalities (e.g., electroreception, Blonder & Alevizon 1988) just prior to prey capture. Because the Atlantic Stingray feeds primarily on benthic infauna, vision does not likely play an important role in prey detection. The Atlantic Stingray possesses anterior horizontal vision, conferring frontal vision, and dorsal binocular vision, conferring good dorsal vision, which is good for overhead predator detection, and a short convergence distance, allowing binocular vision at close distances (McComb & Kajiura 2008). Of the batoid species tested, the Atlantic Stingray had one of the broadest binocular fields, one comparable to species with nearly frontal-facing eyes (e.g., *Rana pipiens*, 90 degrees, Grobstein et al. 1980). The slight canting of the eye of *D. sabina* and retracted skin surrounding the anterior portion of the eye contributed to the large anterior binocular field. The large anterior binocular vision is beneficial as the Atlantic Stingray negotiates turbid shallow coastal lagoons with sea grass and sandy bottoms (Snelson et al. 1988) but is coincident with large blind areas behind the head. The Atlantic Stingray also had the largest monocular visual field measured (McComb & Kajiura 2008).

Electroreception

Elasmobranch fishes possess a sensitive electrosensory system that is used to detect weak electric fields (<0.5 nV cm^{-1}) from prey, predators, and heterospecifics in the surrounding environment. This system also is hypothesized to aid in geomagnetic orientation and navigation (Paulin 1995). The electrosensory system consists of hundreds to thousands of electroreceptive organs (ampullae of Lorenzini) that are grouped into three to five subdermal clusters covering the body of batoids (Fig. 4.7). The ampulla consists of alveolar sacs with a narrow canal that ends on the skin surface with a pore; this canal contains cells that are bound by tight junctions, which forms a higher impedance electrical barrier than the gel within the canal (McGowan & Kajiura 2009). In addition, the lumen is lined by an epithelium of sensory and support cells (New & Tricas 2001).

In laboratory experiments, the electroreceptive ability of Atlantic Stingrays was demonstrated using electrodes and live animals. Atlantic Stingrays made consistent feeding attempts on hidden agar-covered electrodes producing a 5–14 mV cm^{-1} field potential (Blonder & Alevizon 1988). When live invertebrates were concealed and enclosed in the agar chambers, 151 feeding attempts were made out of 213 observed encounters. The experiments did not show the Atlantic Stingray could discriminate between the electric fields of prey (shrimp, *Penaeus* spp.) and non-prey (tunicate, *Mogula* spp.), but the results on discrimination were somewhat inconclusive.

An ontogenetic shift in electroreceptive properties occurs in Atlantic Stingrays with increases in electrosensory primary afferents of resting discharge variability, best frequency, and neural sensitivity, and a decrease in bandpass from the juvenile stage to the adult stage (Sisneros & Tricas 2002). The coefficient of variation of resting discharge activity for neonates (0.233±0.008 SE) was higher than that for juveniles (0.166±0.018 SE) and adults (0.163±0.008 SE). Best frequency of electrosensory primary afferents also differed among ontogenetic stages. Best frequency for neonates and juveniles was lower than that of adults. Only 10% of adult units had best frequencies ≤5 Hz, but 77 and 80% in neonates and juveniles, respectively, had best frequencies ≤5 Hz. In addition, neonates and juveniles were more sensitive to frequencies <3 Hz and >20 Hz compared to adults. Neural sensitivity (gain) of electrosensory primary afferents at best frequency increased with size (disc width) from the neonate to the adult life history stage. Sensitivity at best frequency ranged from 1.2 to 2.3 spikes s^{-1} μ V cm^{-1} for neonates, from 3.1 to 7.6 spikes s^{-1} μ V cm^{-1} for juveniles and from 3.6 to 12.5 spikes s^{-1} μ V cm^{-1} for adults. Neural sensitivity increased about fourfold at best frequency during development from neonate to adult.

Peak sensitivity of electrosensory primary afferents in embryonic Skates matches the frequency band of phasic electric stimuli found in potentials produced by fish predators (1–2 Hz) and corresponds to the same frequency stimuli that interrupt respiratory movements and elicit an anti-predator freeze response. At about 14 cm DW, neonates vacate the shallow sea grass beds and move into deeper waters at about the time when electrosensory afferents show an increase in discharge regularity, best frequency, and neural sensitivity at best frequency. These ontogenetic changes in the response dynamics of the Stingray electrosensory system should allow juveniles to better exploit periodic electric stimuli that are associated with prey and potential predators. The higher bandwidth and best frequency (6–8 Hz) of adult electrosensory primary afferents is near the frequency range associated with the rhythmic alternating current field potentials of small prey items (e.g., amphipods). In sum, the electroreceptor ontogenetic shifts mirror the functionality of the electroreceptor in neonates, juveniles, and adults with the primary function in adults being the location of prey items and mates and the primary function in neonates and juveniles being the avoidance and detection of large predators (Sisneros & Tricas 2002).

Male Atlantic Stingrays use their ampullary electrosensors to locate mates, and their electrosense shifts with levels of androgens. Seasonal changes include a decrease in discharge variability of the electrosensors, an upward shift in best frequency, and a decrease in bandpass (Sisneros & Tricas 2000). A decrease in discharge variability coincides with the onset of spermatocyte production and the annual peak in serum gonadal steroid levels for the population (Tricas et al. 2000). A decrease in the discharge variability of electrosensory primary afferents may facilitate the encoding of low-frequency information. Relative to irregularly discharging units, electrosensory primary afferents that discharge with a relatively high level of certainty (i.e., low endogenous variance) can encode changes in slowly varying electric fields, like those of a ventilating but visually cryptic, buried female. In addition to annual changes in discharge variability, seasonal changes in best frequency and bandpass of electrosensory primary afferents resulted in increased sensitivity to low frequencies from 0.01 to 2 Hz during the primary androgen increase. These are within the frequencies of natural electric signals fields produced by conspecifics (0.25–2 Hz). Thus, the androgen-induced changes in the response properties of ampullary electrosensory primary afferents are apparently an adaptation of the male electrosensory system to enhance the probability of mate detection and the detection of other males, which may be a target of intra-sexual aggression during male competition for access to females (Sisneros & Tricas 2000).

Unlike the River Stingrays (New & Tricas 2001), the euryhaline Atlantic Stingray shows no differentiation in the morphology of the electroreceptors from that of marine elasmobranchs (Whitehead 2002), but the electrosensitivity of the species is dramatically reduced in fresh water relative to sea water. To elicit a feeding response, Atlantic Stingrays in fresh water required an electric field 200–300 times greater than individuals tested in brackish and salt water. In addition, the maximum orientation distance to an electric signal was reduced from 44.0 cm in brackish and salt water to 28.5 cm in fresh water. The reduction in sensitivity in fresh water is attributable to a decrease in electrical resistivity of the water and the physiological function of the ampullary canals. Even so, no difference exists in the electrosensitivities between marine populations and freshwater populations of Atlantic Stingrays when tested at the same salinity. The ability of the electrosensory system to function across a wide range of salinities demonstrates a relative plasticity and the adaptive nature of the electrosensory system within the species (McGowan & Kajiura 2009).

BEHAVIOR

Movement and Diel Activity Patterns

The Atlantic Stingray is variable in its tendency to move, but most movement is associated with temperature-induced seasonal movements across its range. Temperature-induced migration occurs in the marine populations along the Gulf and Atlantic Coasts in which individuals move offshore to warmer, deeper waters as the air temperatures cool below about 17°C (see reviews by Snelson et al. 1988 and Gunter 1945; Bigelow & Schroeder 1953a; Sage et al. 1972), but distances moved appear to vary. Overall there is little evidence for significant coastwise migrations. For example, in Indian River Lagoon, an estuary on the Florida coast, the species only moved into deeper parts (holes and channels, 2–6 m deep) of the lagoons in winter where temperatures averaged about 2–5°C warmer than in the shallows. When temperatures rose above 16–17°C, the species moved into shallow waters (<1 m deep), where it was visible and common during spring, summer, and autumn (Snelson & Williams 1981). That population showed high site fidelity. The recapture rate was 37%, and 80% of the recaptures were at the initial tagging site (106 to 338 days at large) (Schmid 1988). In Atlantic Coast populations from North Carolina and Georgia (Schwartz & Dahlberg, 1978), the movement of individuals tagged in North Carolina was generally southerly along the coast from October to December. Two individuals migrated 80 and 97 km from the Cape Fear River to near Myrtle Beach, South Carolina, during autumn and early winter.

Counts of Atlantic Stingrays moving into and out of a tidal creek in the Florida Panhandle indicated a strong predilection to move with the tide (Teaf 1980). During the falling tide the number of outbound Rays gradually increased with increasing current velocity until low tide was approached. Following low tide, the number of inbound Atlantic Stingrays increased with increasing tidal current velocity. In that study, early morning sampling at ebb tides indicated Atlantic Stingrays occupied the tidal creek at night and during the day, depending on the tide.

In an activity analysis of feeding, swimming, and resting during the day in Indian River Lagoon, Florida, about 60% of individuals over sand were feeding, about 20% were swimming, and about 20% were resting (Bradley 1996). Nearly all individuals at the interface between open sand flats and sea grass beds were feeding. In the sea grass beds, fewer individuals occurred than were expected, and activity was split about equally between swimming and feeding. Frequency of capture by various methods and stomach contents (see ecology section) in the lagoon indicated that Atlantic Stingrays were equally active at day and night (Snelson & Williams 1981; Bradley 1996). The Atlantic Stingray often buries itself in sand to avoid predator detection while resting; if startled it will elevate its venomous spine in defense.

Schooling Behavior

Although concentrations of Atlantic Stingrays are sometimes observed, this most likely is a reflection of suitable habitat and attendant food abundance. Sage et al. (1972) stated that aggregations observed during February and March along the Texas coast represented breeding populations. Whether this was based on evidence or was merely an assumption is unknown. In contrast, the Cownose Rays (genus *Rhinoptera*) undertake regular seasonal migrations involving large numbers of individuals (Schwartz 1990).

REPRODUCTION

The reproduction of *Dasyatis sabina* is of particular interest since it is one of only a few essentially marine chondrichthyan species known to have established reproducing populations in both freshwater and marine environments (Johnson & Snelson 1996). As is true of other chondrichthyans, all dasyatids have internal fertilization, which is accomplished by insertion of the pelvic claspers of the male into the cloaca of the female. All species are ovoviviparous and without placentas, the young (ranging from one to nine) remaining in the female oviducts until they are fully formed; the gestation period lasts up to a year.

Size at Sexual Maturity

Females begin maturation (on the basis of developing ova) at about 22–24 cm DW (Lewis 1982; Snelson et al. 1988; Johnson & Snelson 1996; Table 4.1). Males begin maturation (on the basis of active spermatogenesis) between 20.5 and 25 cm DW (Lewis 1982; Snelson et al. 1988; Johnson & Snelson 1996).

Sexual Dimorphism and Ecomorphological Shifts

Atlantic Stingrays show sexual dimorphism in size, shape, external and internal morphology, and dentition. Females tend to be larger than males, and males typically have arched jaws and a more acute snout and undulated disc. In males the median portion of the pelvic fin forms a paired cylindrical intermittent organ (claspers) that is used in the transfer of sperm during reproduction (Piercy et al. 2006a). The claspers have an associated gland, the clasper gland, which shows increases in fluid production during the breeding season. The fluid, which contains polysaccharides and glucosaminoglycans, may function in sperm suspension and transport, may coagulate sperm to form a congealed covering over the clasper groove to protect sperm from sea water, or may form a copulatory plug aiding in fertilization and blocking competitor's sperm after copulation (Piercy et al. 2006a; see also Piercy et al.

2003). Males also have an alkaline gland, an apparently unique feature of Skates and Rays (Grabowski et al. 1999). The alkaline gland of the Atlantic Stingray consists of a pair of bladder-like, blind-ended, fluid-containing sacs ventral to the posterior of the kidney and lateral to and joined via a duct to the sperm duct (vas deferens). The fluid in the gland is alkaline (pH 8.0–8.2), hence the name, and deep burgundy in color; in Skates the fluid is clear to slightly yellow. The alkaline fluid enters the sperm duct and intermixes with sperm; it appears to increase sperm motility and hence fertilizations (Luer et al. 2007). The fluid also contains a unique relaxin-like molecule, a peptide hormone implicated in parturition in mammal females, which does not affect sperm motility (Büllesbach et al. 1997) but might act on other aspects of sperm function (Grabowski et al. 1999).

Female Stingrays possess a smooth, molariform dentition that is optimal for feeding on hard-shelled bivalves and crustaceans, and males possess a sharp cuspidate dentition optimal for gripping females during copulation (Bigelow & Shroeder 1953a). This character is not fixed, however, because male dentition shifts periodically from molariform to recurved cuspidate dentition (Fig. 4.8) during the reproductive season. This likely occurs because the molariform dentition is optimal for feeding (Kajiura & Tricas 1996).

Spawning and Parental Care

Fertilization for the Atlantic Stingray is internal with the male placing his claspers near the cloaca of the female. The ends of these claspers (tiny hook-like structures with spines) open during copulation, allowing for continuous contact within the female during the transferring of semen. The female houses the developing embryos, which are nourished via an egg yolk until around 60 days of development, after which they gain nourishment from uterine milk and gas exchange occurring in the female's body.

Seasonality

Both freshwater and marine populations of the Atlantic Stingray reproduce on an annual cycle (Breder & Krumholz 1941; Murray & Christmas 1968; Sage et al. 1972; Schwartz & Dahlberg 1978; Lewis 1982; Snelson et al. 1988; Johnson & Snelson 1996; Table 4.1). Vitellogenesis begins around November with ovarian eggs reaching maximum size in early April followed by ovulation; the majority of females complete ovulation and fertilization between early and mid-April (Johnson & Snelson 1996).

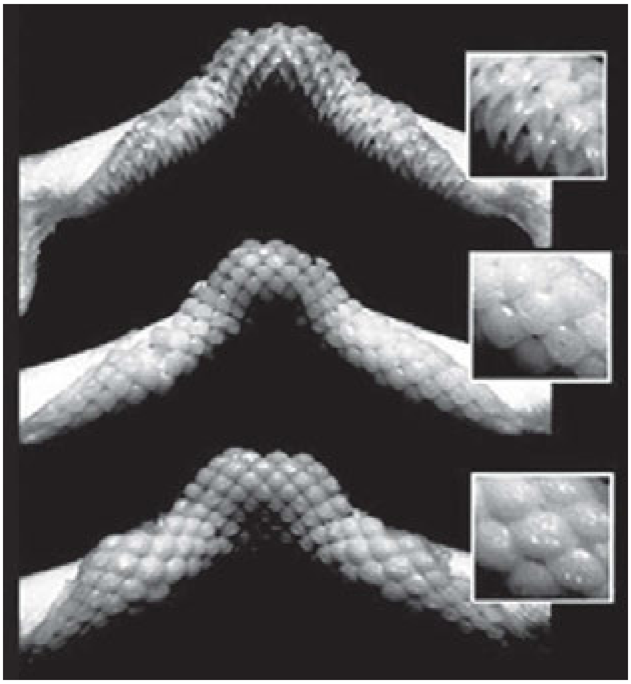

Figure 4.8. Upper jaw dentition of a male Atlantic Stingray, *Dasyatis sabina*, sampled during the mating season (*top*). The cuspidate dentition is evident not only in the first 3–4 rows of functional teeth but also in the developing teeth beneath the dental membrane. In contrast, the upper jaw dentition of a male sampled during the non-mating season (*middle*) is molariform and similar to the female dentition (*bottom*), which does not vary seasonally. Insets show enlarged views of the teeth (photograph courtesy of and used with permission of ©Stephen M. Kajiura).

Hormone Shifts

In a *Dasyatis sabina* population along the east coast of Florida, a single, synchronized reproductive cycle occurred each year with parturition confined to July and August (Snelson et al. 1988). The mating season began in August and continued throughout April, representing a long, protracted mating season with no evidence of sperm storage. Yet, during this 7-month pre-ovulatory mating period, annual cycling of the gonadal steroids testosterone (T), dihydrotestosterone (DHT), 17β-estradiol (E_2), and progesterone (P_4) occurred in both males and females of estuarine populations in conjunction with changes in the reproductive biology, gametogenesis, and sexual behavior. The first increase in male T levels occurred in August, which marks the beginning of the mating season; courtship occurs a month after the initial testosterone increase (September). In October, T, E_2, and P_4 peaked in males, which marked the beginning of copulation; all three levels dropped off around May. In females, T, E_2, and P_4 increased in March, which marked the beginning of ovulation. In addition, E_2 and P_4 increased in July when parturition occurred (Tricas et al. 2000).

Distinct differences in steroid levels and cycles occur between the estuarine populations sampled and those sampled from freshwater Lake Monroe populations in the St. Johns River, Florida. Males within the Lake Monroe population did not show the primary androgen rise as seen in the estuary population that occurred from August to October. The cause of the difference is not directly known but most likely is related to different steroidogenic levels of the spermatocytes or sertoli cells. In addition, the annual E_2 production differs between the two populations. The annual timing of the E_2 surge is similar in both populations, but the magnitude between the populations is markedly different with the estuary population's levels being three times that of the Lake Monroe population. In addition, the E_2 production throughout the entire year is lower for the Lake Monroe population in relation to the estuarine population. In females of the estuarine population, a late summer E_2 surge occurred, but this surge occurred in the middle of the summer in the Lake Monroe population. These differences between the populations suggest that steroidal cycling could possibly be related to osmotic or environmental influences as seen in other organisms (Snelson et al. 1997; Tricas et al. 2000).

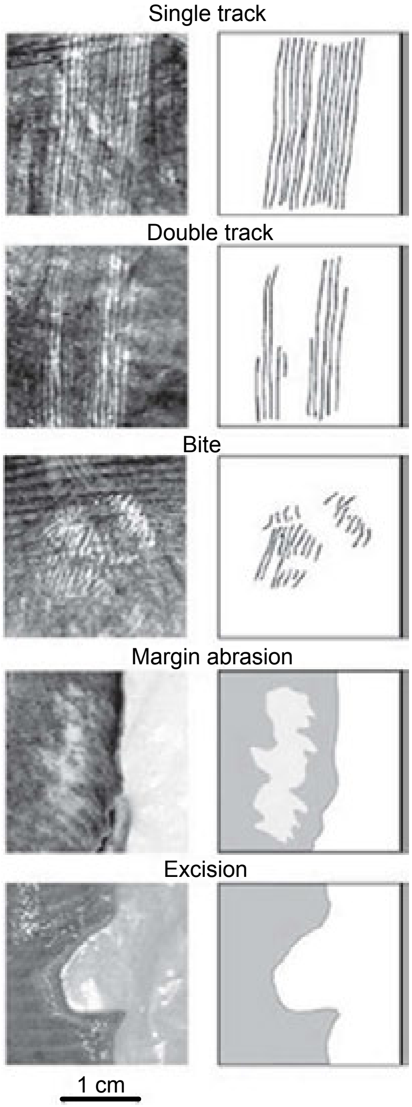

Figure 4.9. Classification of dermal bite wounds on Atlantic Stingrays, *Dasyatis sabina*. Five classes of wounds are identified: single track, double track, bite, margin abrasion, and excision. A photographic image of each wound type is shown on the left and a schematic representation to the right (partially redrawn from Kajiura et al. 2000; photographs courtesy of and used with permission of ©Stephen M. Kajiura).

In addition, the level of the thyroid hormone triiodothyronine (T_3) in females varies significantly in relation to the reproductive cycle. Females undergoing oogenesis have the lowest levels of circulating T_3, and mature females, during the period of ovulation to gestation, have the highest levels of circulating T_3. This indicates that thyroid activity is increased during ovulation and throughout gestation. Males exhibit thyroid hormone levels comparable to that of an immature female. The difference between immature females and mature females is hypothesized to be the presence of vitellogenin in the mature females, which affects the transport and binding of the thyroid hormones (Volkoff et al. 1999).

Courtship

The Atlantic Stingray, in conjunction with most elasmobranchs, exhibits biting behavior during courtship with the male attaching to the pectoral disc of the female (Fig. 4.9). Biting by male Sharks is believed to be a pre-copulatory releasing mechanism in females that stimulates cooperation to mate (Springer 1960).

Reproductive Behavior

Most elasmobranchs exhibit aggressive social interactions between males and females that can last weeks or even months (Tricas 1980). The Atlantic Stingray begins this aggressive behavior in late August with the males chasing and biting fins of both females and males (Fig. 4.9) (Kajiura et al. 2000). Female Rays flee or fend off aggressive males during the long (9 months), protracted mating period as a behavioral means of mate choice (Tricas et al. 2000).

Fecundity

The Atlantic Stingray has relatively small broods. The St. Johns River population had an average brood size of 2.3 young / individual female; no females had >3 young (Johnson & Snelson 1996; Table 4.1). Brood sizes for the marine populations are similar with females having average brood sizes of 2.09 young in the Mississippi Sound (Murray & Christmas 1968), 2.0 in the northeastern Gulf of Mexico (Lewis 1982), and 2.6 in the Indian River Lagoon (Snelson et al. 1988).

Embryonic Development

During its early life the Atlantic Stingray, like most Stingrays, undergoes radical changes in morphology primarily associated with dorsoventrally flattening and disc formation (Lewis 1982). The only complete summary of embryonic development in *Dasyatis sabina* appears to be the unpublished study by Lewis (1982), which was based on specimens from the northeastern Gulf of Mexico. The following, which is taken from Johnson & Snelson (1996), is based on the freshwater population in the St. Johns River.

Embryos were first recognized macroscopically on 15 May, about 4–6 weeks after ovulation and (presumed) fertilization. The earliest developing embryo examined was 1.2 mm DW, or 8.6 mm TL, and weighed 0.004 g. At this early stage of development, pectoral and pelvic fins had not yet developed, and the embryo had an elongate, "shark-like" appearance. The eyes had not yet developed, and the olfactory bulb of the head was enlarged slightly. Only minute signs of external gill filaments were apparent. The weight of yolk from this embryonic stage averaged 0.733±0.080 g, nearly 10 times the weight of the embryo. At 1.8 mm DW, the pectoral fins were beginning to expand laterally, but were restricted to the posterior half of the body. At this stage the cephalic region was ventrally flexed, and the external gills were further enlarged. At about 3.6 mm DW, pelvic fins began development, and the pectoral fins had begun to expand anteriorly. By 5.0 mm DW the eyes began to form, and at 7.0 mm DW, the eyes were pigmented. By 7.0 mm DW the cephalic region became more dorsoventrally flattened. Growth of the embryo during this stage of development was rapid. The mean embryo weight increased from 0.073±0.080 g on 15 May to 9.018±4.380 g on 4 June, a greater than 100-fold increase in an 18-day period.

By 4 June, embryos were well developed; the pectoral and pelvic fins, spiracles, eyes, and mouth were fully formed. Further development was primarily an increase in size rather than conspicuous morphological changes. Up to about 60 mm DW and 11.0 g weight, the external gill filaments were greatly enlarged in embryos. In specimens >11.0 g, the external gill filaments were reabsorbed. The tail spine first began to appear in embryos about 60 mm DW, but did not become hardened until about 70 mm DW (20 June), when embryos were morphologically similar to adult Rays. The rate of growth from 4 June until parturition was less rapid than during the preceding interval. About a twofold increase in weight occurred between both of the semi-monthly collections from 4 June to 3 July. This rate of weight increase was smaller than that occurring earlier in development, but it represented a large increase in embryo mass. The mean weight gain during the 2-week period from 20 June and 3 July accounted for 42% of the mean weight of the embryo at parturition. Weight increased only 20% during the last 2 weeks of gestation. In the 4 June and subsequent collections, the gender of embryos was identifiable by the presence or absence of claspers, which could be seen at 40 mm DW. Of embryos that could be sexed, the sex ratio was 26F:19M, not significantly different from 1:1 ($X^2 = 1.089$, df = 1, $P < 0.297$). Of embryos sampled on 20 June, males were slightly heavier and had larger disc widths than females. In the other three embryo collections, the average female embryo was significantly larger than the average male embryo. Female embryos were significantly heavier than the males (from 4 June to 17 July; 2-way ANOVA: $F = 5.906$, $P = 0.020$). The same results were obtained using embryo DW as the dependent variable. Embryo DW measurements by gender were (mean in mm±SD): 4 June, male 46.9±5.11 (n = 5), female 55.4±10.02 (n = 12); 20 June, male 73.8±4.73 (n = 5), female 70.4±7.05 (n = 8); 3 July, male 86.9±10.49 (n = 7), female 100.2±4.26 (n = 3); 17 July, male 91.4±5.09 (n = 2), female 99.9±8.37 (n = 3).

ECOLOGY

Habitat

The Atlantic Stingray occurs in brackish bays and estuaries with a permanent freshwater population known to exist in the St. Johns River, Florida (McLane 1955; Tagatz 1968; Johnson & Snelson 1996). The marine populations occur in shallow, inshore regions over sand flats or sand-silt substrates in water <25 m deep (Snelson et al. 1988; Table 4.1). In a habitat-use assessment in Indian River Lagoon, Florida, more Atlantic Stingrays occurred within sand habitats (51%) than sea grass beds (31%) or the interface between the two habitats (31%) (Bradley 1996). The freshwater population occurs in shallow water (1–2 m deep) with a soft, mud bottom mixed slightly with sand toward the littoral zone (Johnson & Snelson 1996).

Diet and Feeding

The Atlantic Stingray is a benthic forager that feeds primarily on small crustaceans, polychaete worms, and other small invertebrates associated with the bottom (Gunter 1945; Bigelow & Schroeder 1953a; Funicelli 1975; Cook 1994; Bradley 1996; Boschung & Mayden 2004). Excavation of the substrate is accomplished by flapping the wing-like pectoral fins, an action that exposes the invertebrate prey that composes the bulk of the diet (Boschung & Mayden 2004). The resulting feeding pit appears as a sharp-edged hole that is <10 cm in diameter and depth (Bradley 1996). In Indian River Lagoon, Florida, more feeding pits occurred in open sand flats than sea grass beds relative to the availability of those habitats. Diel stomach analyses in summer indicated feeding was continuous throughout a 24-h period, and over that period, no shifts in intensity of feeding were detected. In that system, six taxonomic groups (amphipods, isopods, ophiuroids, mysids, polychates, and bivalves) constituted 98% of the diet by number. Amphipods and isopods accounted for >50% of the prey in these groups (Cook 1994; Bradley 1996). Amphipods dominated the summer diet when they were apparently preferentially selected (Bradley 1996). Fishes, especially Bay Anchovies (*Anchoa mitchilli*) and Atlantic Croakers (*Micropogonias undulatus*), were sometimes eaten, and squid were also taken as an occasional food item. Within the Indian River Lagoon system, the diet consisted primarily of pistol shrimp and a variety of polychaete worms (Snelson & Williams 1981). Further, Atlantic Stingrays exhibit higher absorption rates of food while in lower-temperature waters due to the lower evacuation rate of the ingested food (Di Santo & Bennet 2011).

Age and Growth

Although several ecological studies involving *Dasyatis sabina* are available (Sage et al. 1972; Schwartz & Dahlberg 1978; Johnson & Snelson 1996), and Johnson & Snelson (1996) presented data on embryonic growth (see previous), no published information is available on subsequent age and growth or maximum longevity. Tagging studies aimed at obtaining age-growth data were attempted on Florida populations, but these proved inconclusive (F. F. Snelson pers. comm.). In that study in the Indian River Lagoon, Florida, mean growth of captive neonates over 1 year was 3.6 mm/month (Schmid 1988). Mean weight gains averaged 14.5 g/month in females and 11.4 g/month in males. Growth functions estimated from a tag-recapture study suggested a maximum size of 340 mm DW, slightly less than the observed maximum size in the Indian River population of 370 mm DW (2.2 kg) (Snelson et al. 1988). The largest male observed was 370 mm DW (1.6 kg). After about 200 mm DW males are slightly heavier than females. Nearly all of the largest individuals (>270 mm DW) were females (Schmid 1988; Snelson et al. 1988). Rings on vertebral centra ranged from 2–9 for males and 6–12 for females, but whether ring formation was annual or not was inconclusive (Schmid 1988).

Ontogenetic Shifts in Habitat Use

Size frequency data are suggestive that in some populations habitat shifts occur with growth. Juveniles (160–200 mm DW) were taken in low frequencies in studies in Indian River Lagoon, Florida (Schmid 1988; Snelson et al. 1988), and the Cape Fear River (Schwartz & Dahlberg 1978) despite the use of capture gear and techniques that were effective in taking other sizes of Atlantic Stingrays (e.g., trawls, gillnets, seines). Although the evidence is far from conclusive, juveniles may be using deeper or at least different habitats than adults. In any case the deficit of juveniles in samples is enigmatic (Snelson et al. 1988).

Effects on Prey

Rays can alter the community structure through mechanical excavation of benthic substrates. In the Atlantic Stingray a patch of sediment could be excavated once every 70 days, creating a disturbance event that leads to infaunal recolonization. Nevertheless, harpacticoid copepod communities in disturbed sites were indistinguishable from undisturbed sites 29 h after the disturbance (Reidenauer & Thistle 1981). With this relatively high turnover rate, Atlantic Stingrays most likely alter large-scale habitat and may smooth distributions of infaunal invertebrates (Hines et al. 1997), suggesting that digging Rays, such as the Atlantic Stingray, can structure benthic communities in many locations (VanBlaricom 1982).

Parasites

Elasmobranch species offer a multitude of sites that can be parasitized by metazoan parasites. Six phyla are most common as parasites within elasmobranchs (i.e., Platyhelminthes, Arthropoda, Nematoda, Annelida, Acanthocephala, and Mollusca) with the phyla Platyhelminthes and Arthropoda representing the most diverse parasites. The Atlantic Stingray is no exception, containing many parasites spanning the phyla Platyhelminthes, Annelida, and Arthropoda. Common parasites found include the platyhelminths *Entobdella corona* and *Prochristianella penaei* and *Thaumatocotyle* (Hutton 1964; Aldrich 1965; Euzet & de Buron 2010); the annelids *Branchellion ravenelii* and *Myliobaticola richardheardi* (Hutton 1964; Bullard & Jensen 2008); and two parasitic copepods (Arthropoda), *Brachiella concava* and *Caligus praetextus* (Hutton 1964). A main parasite of the freshwater Atlantic Stingray is the genus *Argulus*, a fish louse that feeds on the skin mucus (Passarelli & Piercy 2009).

Predators

The Atlantic Stingray, as well as other Stingrays living in shallow marine water, are a common food item for inshore Sharks, as attested by spines found embedded in the stomachs of such species as Tiger Sharks (*Galeocerdo cuvier*), Lemon Sharks (*Negaprion brevirostris*), Bull Sharks (*Carcharinhus leucas*), and Blacktip Sharks (*Carcharhinus limbatus*) (Bigelow & Schroeder 1953a). In addition, Great Blue Herons off the coast of Mississippi consumed Atlantic Stingrays residing in marine waters (Ajemian et al. 2011). In freshwater habitats American Alligators (*Alligator mississippiensis*) prey on Atlantic Stingrays (Passarelli & Piercy 2009).

CONSERVATION

No fishery directly targets *Dasyatis sabina*, but Atlantic Stingrays are caught as bycatch in gillnets, Shark drift nets, and nearshore trawls that target commercially important species (although because most are released alive there is minimal impact on their population numbers) (Piercy et al. 2006b). Yet, the freshwater population of the Atlantic Stingray has declined in overall health and reproductive success as water quality has declined within the St. Johns River basin (Passarelli & Piercy 2009). Declines in health may be related at least in part to elevated organochlorine levels in tissues of Atlantic Stingrays that are associated with development in the St. Johns River basin, but reproductive impairment apparently is related to other as yet unidentified ecological factors (Gelsleichter et al. 2006).

COMMERCIAL IMPORTANCE

The Atlantic Stingray is of little or no direct economic importance. It is often caught during commercial fishing operations but is normally discarded as part of the bycatch. No fishery targets Atlantic Stingray and the bycatch mortality is considered low, resulting in an assessment label of Least Concern by the International Union for Conservation of Nature. Skates, and to a lesser extent Stingrays, are sometimes retained for the purpose of punching out circular sections of the wings, which are marketed as scallops. Because of its small size, *Dasyatis sabina* is rarely if ever used for this purpose. The species is of scientific interest because as a marine species it can live and sometimes spend its entire life in fresh water. The Atlantic Stingray also has scientific value in comparative studies of the evolution and function of genes and physiological systems (e.g., see physiology section).

LITERATURE GUIDE

Bigelow and Schroeder's (1953a) guide, *Fishes of the Western North Atlantic: Sawfishes, Guitarfishes, Skates, Rays, and Chimaeroids*, provides a still useful, albeit somewhat dated, overview of the Atlantic Stingray, including distribution and habitat. Boschung & Mayden (2004) also provide a good summary of the species and its biology. The works by F. F. Snelson Jr. and colleagues provides an excellent framework for both the ecology and reproduction of the freshwater populations (references in text). T. C. Tricas, J. S. Sisneros, S. M. Kajiura, and K. P. Maruska provide in-depth research of the mechanosensory and electrosensory systems within the Atlantic Stingray (references in text). In addition, T. C. Tricas, S. M. Kajiura, and K. P. Maruska cover, in great detail, the reproductive behavior and mating strategies for the Atlantic Stingray (references in text). For detailed information concerning the osmoregulation within the freshwater population, consult the work of P. M. Piermarini and colleagues (e.g., Piermarini & Evans 1998; Piermarini & Evans 2000; Piermarini & Evans 2001; Piermarini et al. 2002).

Acknowledgments

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Chapter 5

Acipenseridae: Sturgeons

Bernard R. Kuhajda

The Acipenseridae consist of 25 extant species in 4 genera, including 17 species in *Acipenser*, 2 in *Huso*, 3 in *Pseudoscaphirhynchus*, and 3 in *Scaphirhynchus* (Birstein & Bemis 1997; Birstein et al. 1997a; Billard & Lecointre 2001; Ludwig 2008). The word “acipenser” is the Latin name for Sturgeon. Sturgeons occur on all continents in the Northern Hemisphere and are almost completely restricted to the northern temperate zone (Bemis & Kynard 1997; Choudhury & Dick 1998). The greatest diversity of Sturgeons is in western Europe (11 species) and central Asia, including the Mediterranean, Aegean, Black, Caspian, and Aral Seas, which is referred to as the Ponto-Caspian region (Bemis & Kynard 1997). Five species of *Acipenser* and three species of *Scaphirhynchus* occur in North America. Sturgeons are the largest freshwater fishes and are long-lived (e.g., >150 years old). Originally described as Sharks in the 1700s due to the cartilaginous skeleton, jaw structure, and shark-like tail, Sturgeons are actually ancient bony fishes with fossils that date to 175 mya. They have a toothless, protrusable mouth on the underside of the head with four barbels just before the mouth and five rows of bony plates along the body. Sturgeons cruise along the bottom of rivers, lakes, and oceans, locating and eating invertebrates and fishes from the bottom with the aid of taste buds on the barbels and ampullary organs on the underside of the head, which use electroreception to detect the weak electrical fields emitted by prey. Although some Sturgeons spend most of their lives in the oceans or estuaries, they all spawn in freshwater rivers where they were hatched, some migrating ≤1,200 km (746 miles) to spawn. Newly hatched larvae passively drift in river currents ≤530 km (329 miles). Sturgeons are highly vulnerable to human activities, especially overfishing and dams that block migratory routes; therefore, almost all Sturgeons worldwide are considered imperiled. Their roe (eggs), which are processed into caviar, have been valued by humans for >1,000 years.

DIVERSITY AND DISTRIBUTION

In North America, Sturgeons occur along both coasts and in inland fresh waters (Figs. 5.1 and 5.2). Two species of *Acipenser* (Fig. 5.1), the Green Sturgeon (*Acipenser*

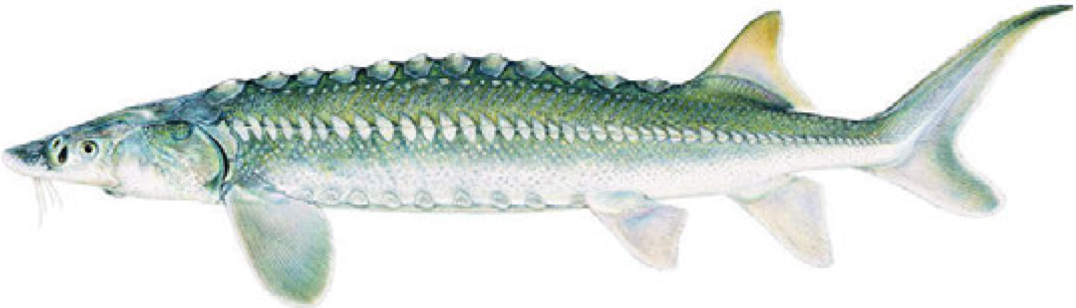

Plate 5.1. White Sturgeon, *Acipenser transmontanus*

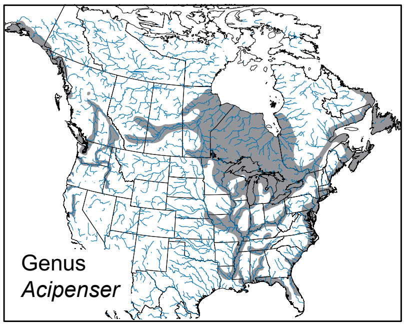

Figure 5.1. Geographic range of *Acipenser* in North America.

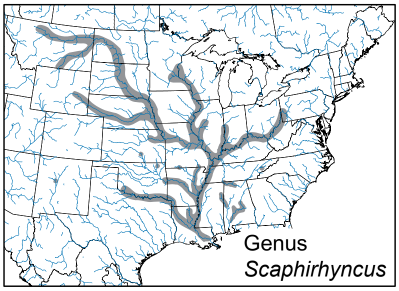

Figure 5.2. Geographic range of *Scaphirhynchus*.

medirostris) and the White Sturgeon (*Acipenser transmontanus*), are restricted to the North Pacific region. Green Sturgeons occur along 3,000 km (1,864 miles) of coastal and estuarine areas from the Aleutian Islands, Alaska, to central California, and into Mexico (Lee et al. 1980; Page & Burr 1991; Moyle 2002; Wilson & McKinley 2004; Nelson et al. 2004). The White Sturgeon was once considered one of the few Sturgeon species found on two continents with an Asian distribution in China, northern Japan, Korea, and Russia north to the Amur River, but karyotypic and genetic data indicate that the Asian distribution represents a separate species, the Sakhalin Sturgeon (*Acipenser mikadoi*) (Birstein & Bemis 1997). White Sturgeons inhabit coastal areas from the Aleutian Islands, Alaska, to central California with a landlocked population naturally isolated by falls in the Kootenai River in the upper Columbia River drainage in Idaho, Montana, and British Columbia (Lee et al. 1980; Page & Burr 1991, 2011; Anders et al. 2002; Wilson & McKinley 2004).

The Western Atlantic region is home to two species of *Acipenser*, the Shortnose Sturgeon (*Acipenser brevirostrum*) and Atlantic Sturgeon (*Acipenser oxyrinchus*) (Fig. 5.1). Shortnose Sturgeons inhabit coastal waters along the eastern seaboard from New Brunswick, Canada, to northern Florida. Two subspecies of the Atlantic Sturgeon are recognized. The nominate form, *A. oxyrinchus oxyrinchus*, is distributed along the Atlantic Coast from northern Quebec and Newfoundland, Canada, to northern Florida. The Gulf Sturgeon (*A. oxyrinchus desotoi*) is restricted to coastal areas in the Gulf of Mexico from Tampa Bay, Florida, to Louisiana, and perhaps westward to the Rio Grande, Texas and Mexico (Lee et al. 1980; Page & Burr 1991; Wilson & McKinley 2004; Nelson et al. 2004).

The Lake Sturgeon (*Acipenser fulvescens*) (Fig. 5.1) and all species of *Scaphirhynchus* (Fig. 5.2) occur in fresh water in middle North America. The Lake Sturgeon is found in lakes and rivers from Hudson Bay, Great Lakes, and St. Lawrence River drainages from Alberta to Quebec, Canada, south to the lower Mississippi and Coosa River drainages, Louisiana and Alabama. The Alabama Sturgeon (*Scaphirhynchus suttkusi*) is restricted to the Mobile Basin in large rivers in Alabama and formerly in Mississippi. The Pallid Sturgeon (*Scaphirhynchus albus*) is nearly restricted to the Missouri and Mississippi Rivers proper from Montana to Louisiana but does use the lower reaches of major tributaries. The Shovelnose Sturgeon (*Scaphirhynchus platorynchus*) is distributed throughout the Mississippi River basin, including the Missouri and Ohio River drainages, from Montana to Pennsylvania, south to Louisiana, and had a historical population in the Rio Grande, New Mexico (Lee et al. 1980; Page & Burr 1991; Wilson & McKinley 2004; Nelson et al. 2004).

Polyploidization and Diversity

Polyploidization is one of the main genetic mechanisms of speciation within Acipenseriformes (Sturgeons) and has contributed to the diversification within *Acipenser*. The diploid ancestor of all Acipenseriformes had a karyotype of 60 chromosomes that produced a tetraploid (4n) ancestor with 120 chromosomes through a gene duplication event (Birstein et al. 1997b; Ludwig et al. 2001; see genetics

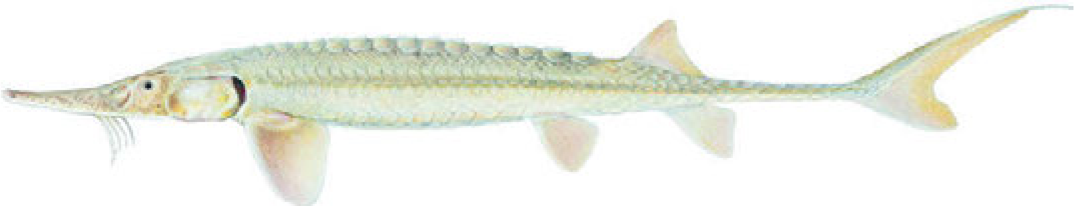

Plate 5.2. Shovelnose Sturgeon, *Scaphirhynchus platorynchus*

section). A diploid condition may have been established in this ancestor before diversification into species of Polyodontidae (Paddlefishes) and Acipenseridae (Ludwig et al. 2001; Fontana 2002), but others consider extant species with 120 chromosomes as tetraploids (Birstein et al. 1997b; Kim et al. 2001). Only species within *Acipenser* have higher chromosome numbers with some species possessing 240–260 (8n) and others having ≤500 chromosomes (16n) (Birstein et al. 1997b; Fontana 2002). Relationships within *Acipenser* based on molecular data indicate that these high-ploidy species arose multiple times (Birstein et al. 1997b; Ludwig et al. 2001), and the likely method was reticular speciation (Vasil'ev 1999). A current model for reticulate speciation involves three steps. Interspecific hybridization between diploid bisexual species forms an all-female diploid species that produces diploid eggs. The all-female species then back-crosses with the parental species, resulting in a triploid unisexual species. Hybridization between the triploid species and a diploid bisexual species results in a tetraploid bisexual species. These intermediate unisexual diploid and triploid species occur in some other fishes, amphibians, and lizards but are not known from Sturgeons (Vasil'ev 1999, 2009). Polyploidization via reticulate speciation may be one of the primary sources of reduced genetic differences between Sturgeon taxa (Robles et al. 2005).

Anadromy and Diversity

Anadromy is likely a secondary adaptation in Sturgeons with ancestors having evolved as freshwater fish. This is supported by several evolutionary life history constraints of Sturgeons (Sulak & Randall 2002). Eggs and larvae of all Sturgeons are intolerant of salt water (Kynard & Horgan 2002a; Kynard & Parker 2004). Juveniles and subadults of anadromous species return in the spring to a physiological refuge that fresh water affords them as they remain relatively dormant with little or no feeding during the warm summer months (Sulak & Randall 2002). Anadromy likely evolved as a means to exploit the marine and estuarine environment where the rich benthic invertebrate resources allow for dramatic increase in growth rates relative to those species foraging in freshwater environments. In Gulf Sturgeons feeding in salt water is confined to winter months when predation threats from sharks and competition from teleosts are lowest (Sulak & Randall 2002). The exploitation of the marine environment by *Acipenser* may be an additional factor linked to the diversity within this genus (Bemis & Kynard 1997).

Evolutionary Rate and Diversity

Although some morphological, genetic, and ecological differences have evolved between Sturgeon genera, and to a lesser extent, among congeners, relatively little change has occurred in Acipenseridae over tens of millions of years. The basic body plan, osteology, and general habitats between extant and fossil Sturgeons from the Upper Cretaceous (about 99.6–65.5 mya) differ little (Bemis et al. 1997; Choudhury & Dick 1998; Hilton & Grande 2006; see fossil record section), and the rate of molecular evolution has been extremely slow for all Sturgeons, resulting in a lack of variation in genetic markers. This slow rate of change is likely due to Sturgeons having long generation times, low metabolic rates, and reduced rates of concerted evolution (Wirgin et al. 1997; de la Herrán et al. 2001; Krieger & Fuerst 2002b, 2009; Robles et al. 2004; Krieger et al. 2006; Dillman et al. 2007).

Relationships among Species

Relationships among species of North American Sturgeons have received considerable attention. Within *Scaphirhynchus*, phylogenetic analysis of morphological data indicated Shovelnose and Alabama Sturgeons were sister-species (Mayden & Kuhajda 1996), but studies based on mitochondrial DNA sequence data were unable to address this hypothesis because of the slow rate of molecular evolution at these genes (Campton et al. 2000; Krieger et al. 2000; Simons et al. 2001). Within *Acipenser*, relationships based on morphological and karyological data show sister-species relationships between the two North American Pacific species, White and Green Sturgeon, and between Shortnose and Lake Sturgeon, with the Atlantic Sturgeon basal to these species (Artyukhin 1995; Choudhury & Dick 1998). Mitochondrial DNA analyses on only North American species showed these same relationships (J. R. Brown et al. 1996; Krieger et al. 2000), but when other species of *Acipenser* are included, these sister-species pairs are not recovered, but each species of the pair typically occur within the same clade (Birstein & DeSalle 1998; Ludwig et al. 2001; Birstein et al. 2002; Artyukhin 2006).

Most species of Sturgeon are identified morphologically using adult characters, such as head and body measurements, including snout shape and eye diameter, as well as barbel placement and the number or type of scutes, squamation, and head spines (Scott & Crossman 1973; Mayden & Kuhajda 1996; Vecsei & Peterson 2004). But differential growth rates of distinguishing characteristics (allometry or heterochrony) can make species identification difficult for larvae, juveniles, and subadults, and other characters, such as spines and scutes, may be obscured or lost in older adults (Jordan & Evermann 1896; Bailey & Cross 1954; Vladykov & Greeley 1963; Scott & Crossman 1973; Mayden & Kuhajda 1996; Gisbert & Doroshov 2006).

Intraspecific Variation

Identification of Sturgeons is further complicated by intraspecific variation in meristic and morphometric characters, especially between populations from separate drainages (Guénette et al. 1992; Keenlyne et al. 1994; Mayden & Kuhajda 1996; Walsh et al. 2001; North et al. 2002). This variation may be a result of strong homing capabilities by spawning adults to natal river systems or sites (Bemis & Kynard 1997). Even within a population, skeletal, rostral, and scute morphologies can show significant variation between specimens at the same life history stages, and skull features can vary between right and left sides within an individual (Hilton & Bemis 1999; Vecsei 1999; Vecsei & Peterson 2004). The large degree of intraspecific variation in Shortnose Sturgeon may be the result of high genetic diversity of founding populations during post-Pleistocene (≤10,000 years ago) colonization of Atlantic systems (i.e., minimal founder effect), resulting from either colonization by individuals from numerous adjacent systems or from glacial refugia that had maintained high haplotype diversity. Alternatively, dramatic declines in Atlantic Coast populations during the late Pleistocene (1.8–0.01 mya) may have caused a genetic bottleneck, making remnant populations susceptible to genetic drift that created morphological divergence (Vecsei & Peterson 2004).

Sturgeons as Non-Natives

Only one species, the White Sturgeon, has been introduced outside its native range. White Sturgeons have been introduced via aquaculture to South America, the Middle East, and Europe. White Sturgeons were introduced in Chile sometime after 1981 and have been found in the Rio Maipo (Dyer 2000); they were found in the wild in Israel in 1997 but are not established (Roll et al. 2007). Introductions in Europe are the result of accidental releases or escapes from aquaculture facilities and perhaps deliberate releases by aquarists (Arndt et al. 2000, 2002). The numbers of exotic Sturgeons have increased substantially since 1990 in Germany, coinciding with the rise of Sturgeon aquaculture and the first importation of White Sturgeons in 1992. They are not considered established because they have not reached maturity, but once mature they may hybridize with the native Sturgeons (Wolter & Röhr 2010); hybridization between native Sterlet (*A. ruthenus*) and introduced Siberian Sturgeon (*A. baerii*) has occurred in the upper Danube River on the Germany-Austria border even though these species differ in chromosome number (118 versus 248, respectively) (Ludwig et al. 2009). Other concerns in Europe include exotic Sturgeons thriving and interfering with restoration of the critically endangered native European Sturgeon (*Acipenser sturio*) and introduction of diseases and parasites. Disease transfer from White Sturgeons is of particular concern given the variety of viruses present in this species (Arndt et al. 2000, 2002), and the White Sturgeon herpes virus occurs in aquacultured White Sturgeons in Italy (Kurobe et al. 2008). From 1991 to 2000 White Sturgeons made up 1% of the total coastal and inland Sturgeon fishery in Poland, Germany, and the Netherlands, first appearing after 1993 in rivers and estuaries. Within the United States, White Sturgeons have been introduced in Arizona (Minckley 1971).

PHYLOGENETIC RELATIONSHIPS

Higher Relationships

Researchers in the mid- to late 1700s considered Sturgeons (and the Paddlefish) closely related to Sharks given their similar jaw structure and cartilaginous skeletons (Linnaeus 1758). This relationship was rejected in the mid-1800s and Sturgeons (and the Paddlefishes) were considered bony fishes (osteichthyans) and placed in the basal grade Chondrostei (Grande & Bemis 1991, 1996; Bemis et al. 1997). Currently Sturgeons (Acipenseridae) and Paddlefishes (Polyodontidae) are placed in the suborder Acipenseroidei, and along with the fossil families †Chondrosteidae and †Peipiaosteidae, are placed in the order Acipenseriformes (Grande & Bemis 1991, 1996; Grande et al. 2002; Grande & Hilton 2006; Krieger et al. 2008; Hilton & Forey 2009; Hilton et al. 2011). Based on the distribution of the fossil families and the greatest current species diversity of the group in the Ponto-Caspian region, the order Acipenseriformes likely originated in Western Europe followed by diversification into central Asia with a later appearance in North America (Bemis & Kynard 1997). Acipenseriformes, Bichirs (order Polypteriformes), and other fossil orders were assigned to the subclass Chondrostei that was basal to all other neopterygian fishes (Nelson 1994). But subsequent studies found that Bichirs are extant basal actinopterygiian fishes (Ray-finned Fishes) (subclass Cladistia), and Acipenseriformes together with other fossil orders form the subclass Chondrostei that is sister to the subclass Neopterygii (Patterson 1982; Bemis et al. 1997; Nelson 2006).

Relationships within Acipenseridae

Several hypotheses exist for the relationships of Sturgeon genera within Acipenseridae (genera *Acipenser*, *Huso*, *Scaphirhynchus*, *Pseudoscaphirhynchus*) (Fig. 5.3). The classic arrangement recognizes two subfamilies: Acipenserinae (genera *Acipenser* and *Huso*) and Scaphirhynchinae (genera *Scaphirhynchus* and *Pseudoscaphirhynchus*) (Berg 1940; Bailey & Cross 1954; Nelson 1994). This classification was supported by a phylogenetic analysis of morphological characters (Fig. 5.3a; Mayden & Kuhajda 1996; Artyukhin 2006). Several osteological studies using extant and fossil materials (Findeis 1993, 1997; Grande & Bemis 1996; Bemis et al. 1997) place *Huso* in the subfamily Husinae that is basal to the subfamily Acipenserinae; Acipenserinae contains the tribe Acipenserini (genus *Acipenser*) that is basal to the tribe Scaphirhynchini (genera *Scaphirhynchus*, †*Protoscaphirhynchus*, and *Pseudoscaphirhynchus*) (Fig. 5.3b). But subsequent studies discovered (1) a new well-preserved Sturgeon fossil, genus †*Priscosturion*, possesses numerous osteological characters previously not discernible in other fossil Sturgeons; (2) some characters from the fossil Sturgeon genus †*Protoscaphirhynchus* are inaccurate (see fossil record section); and (3) some characters thought unique to Sturgeons (e.g., pectoral spines) actually are shared with a primitive fossil Paddlefish (Grande et al. 2002; Grande & Hilton 2006, 2009). These new osteological data place the genus †*Priscosturion* in its own subfamily, †Priscosturioninae, which is basal to the subfamily Acipenserinae that now contains the genera *Acipenser* and *Huso* and the tribe Scaphirhynchini (genera *Scaphirhynchus* and *Pseudoscaphirhynchus*). Placement of †*Protoscaphirhynchus* is uncertain because of its lack of characters (Grande & Hilton 2006, 2009) (Fig. 5.3c).

In contrast to morphological studies, phylogenetic relationships based on mitochondrial DNA sequence place the genus *Scaphirhynchus* (Birstein et al. 1997b, 1999; Birstein & DeSalle 1998; Krieger et al. 2000), the genus *Scaphirhynchus* plus Atlantic-European Sturgeons (Ludwig

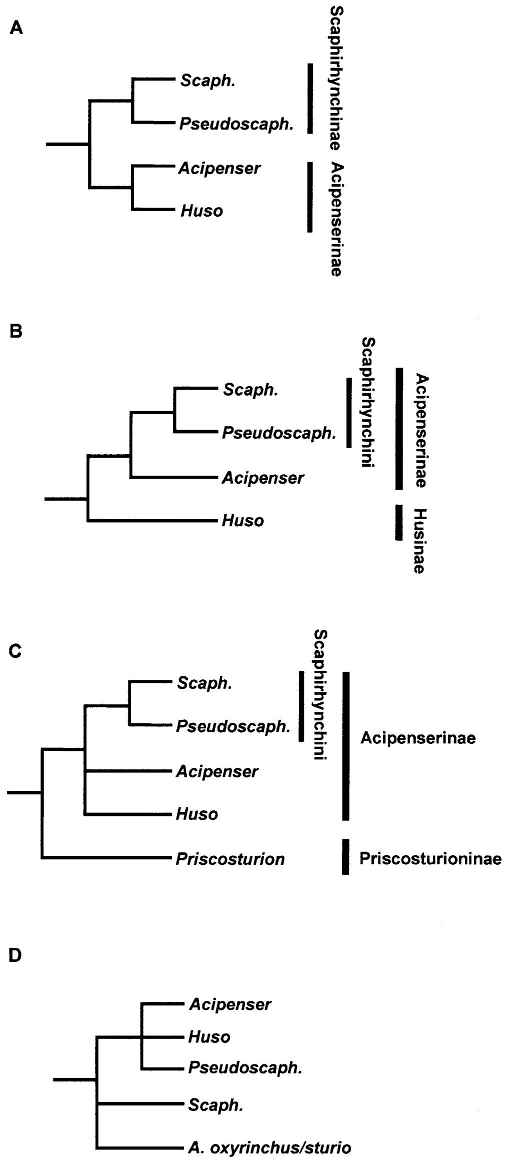

Figure 5.3. Phylogenetic relationships of Sturgeon genera within the family Acipenseridae (genera *Acipenser*, *Huso*, *Scaphirhynchus*, *Pseudoscaphirhynchus*): (A) classic arrangement recognizing two subfamilies Acipenserinae and Scaphirhynchinae (redrawn from Mayden & Kuhajda 1996; Artyukhin 2006); (B) osteological studies using extant and fossil materials recognize the subfamily Husinae basal to the subfamily Acipenserinae, which contains the tribe Acipenserini basal to the tribe Scaphirhynchini (redrawn from Findeis 1993, 1997; Grande & Bemis 1996; Bemis et al. 1997); (C) revised osteological relationships recognize the subfamily †Priscosturioninae basal to the subfamily Acipenserinae, which contains the tribe Scaphirhynchini (redrawn from Grande & Hilton 2006, 2009); and (D) mitochondrial DNA sequence data place the genus *Scaphirhynchus* plus Atlantic-European Sturgeons basal to an unresolved clade of all other Sturgeons (redrawn from Birstein et al. 1997b, 1999, 2002; Birstein & DeSalle 1998; Fontana et al. 2001; Ludwig et al. 2001; Dillman et al. 2007; Krieger et al. 2008). *Scaph.* = *Scaphirhynchus*; *Pseudoscaph.* = *Pseudoscaphirhynchus*.

et al. 2001; Fontana et al. 2001), or either group (unresolved, Krieger et al. 2008) as basal to all other extant Sturgeons. Additionally the subfamily Husinae is not recovered, the genus *Huso* is not monophyletic (Birstein & DeSalle 1998; Birstein et al. 1999, 2002; Ludwig et al. 2001; Krieger et al. 2008), and the genera *Scaphirhynchus* and *Pseudoscaphirhynchus* do not form a distinct subfamily or tribe (Birstein et al. 1997b, 2002; Dillman et al. 2007; Krieger et al. 2008) (Fig. 5.3d). Studies using sequence data from nuclear and nuclear satellite DNA support these relationships (de la Herrán et al. 2001; Robles et al. 2004, 2005; Krieger et al. 2006). Sturgeon relationships as revealed by molecular analyses appear to conform to transoceanic distributions for two major clades (Ludwig et al. 2000, 2001; Birstein et al. 2002; Dillman et al. 2007; Krieger et al. 2008), including the Pacific Sturgeon clade (White and Green Sturgeons, and Asian *Acipenser* and *Huso*) and the Atlantic Sturgeon clade (Shortnose and Lake Sturgeons, and European-Asian *Acipenser*, *Huso*, and *Pseudoscaphirhynchus*). Two other clades also are recognized, the basal sea Sturgeons (Atlantic and European Sturgeons) and the genus *Scaphirhynchus* (Robles et al. 2004, 2005; Krieger et al. 2008). A morphological phylogeny of 23 extant Sturgeon species (no fossils) supported several aspects of these molecular phylogenies, including sea Sturgeons as basal *Acipenser*, an Atlantic-Pacific split for some *Acipenser* species (but only those with ≥250 chromosomes), and lack of support for the subfamily Husinae (containing only *Huso*) but continued to support the monophyly of *Huso* and Scaphirhynchinae (Artyukhin 2006). Studies examining fewer extant Sturgeons but including extensive skeletal characters and fossil taxa were in agreement with molecular phylogenies on a close relationship between *Pseudoscaphirhynchus* spp. and the Stellate Sturgeon, *Acipenser stellatus*, rather than with *Scaphirhynchus*, and designated a new subfamily Pseudoscaphirhynchinae. The subfamily Husinae was also recognized, but only included one *Huso* species and the Sterlet, *Acipenser ruthenus*. The relationships of these clades and the genera †*Priscosturion*, *Scaphirhynchus*, and several other *Acipenser* species were unresolved within Acipenseridae (Hilton 2005; Hilton & Forey 2009; Hilton et al. 2011).

Evolutionary Considerations

The greatest extant Sturgeon species diversity is in the Ponto-Caspian region (Bemis & Kynard 1997; Choudhury & Dick 1998) and biogeographical reconstruction based on a molecular phylogeny of extant Acipenseriformes implies this region was the center of origin for Sturgeons (Peng et al. 2007). Estimates of the divergence time of major Sturgeon lineages using molecular data include the separation of the sea Sturgeons about 171 mya, *Scaphirhynchus* from the remaining Sturgeons nearly 151 mya, and the Atlantic-Pacific split around 121 mya (Peng et al. 2007).

FOSSIL RECORD

†*Priscosturion longipinnis* is the only well-preserved, articulated Sturgeon fossil with a relatively complete skeleton (Fig. 5.4). The single specimen is 80 cm TL and is from the Upper Cretaceous Judith River Formation (about 78 mya), Montana (Grande & Hilton 2006, 2009). The species shares several features with living Sturgeons, including a thick pectoral spine, a cardiac shield formed by the shoulder girdle, a row of dorsal bony plates (scutes) from the back of the skull to the anterior edge of the dorsal fin, and a lateral-line canal system concealed under the lateral scutes. †*Priscosturion longipinnis* differs from living Sturgeons by having more dorsal scutes (20), a trunk almost completely covered with thick scales, and a highly falcate and extremely long dorsal fin (140 fin rays). A phylogenetic analysis of osteological features placed †*P. longipinnis* as basal to all living Sturgeons (Grande & Hilton 2006).

The only other articulated Sturgeon fossil described is †*Protoscaphirhynchus squamosus*, but the specimen is only partially intact and is badly crushed and weathered (Wilimovsky 1956) (Fig. 5.5). The fossil is from the Upper Cretaceous Hell Creek beds (about 65 mya), Montana. Parts of the head, body, and tail are discernible, and the fossil resembles the genus *Scaphirhynchus* but differs in having its entire body covered by plates and scutes (Wilimovsky 1956). Findeis (1993) argued that only the posterior end of the fossil is completely armored, which is similar to *Scaphirhynchus*, and Bemis et al. (1997) suggested †*P. squamosus* may not warrant its own genus. Additionally, Hilton (2004) considered two caudal skeleton characters as shared between †*Protoscaphirhynchus* and *Scaphirhynchus*. In contrast, Gardiner (1984) did not consider †*P. squamosus* an Acipenseriformes based on scale type and skull features. This fossil was used in several phylogenetic studies of Sturgeons and of lower actinopterygians (Findeis 1993; Grande & Bemis 1996; Bemis et al. 1997; Jin 1999), but some characters detailed in the original description are questioned in a redescription of this fossil species (Hilton & Grande 2006) in which only the

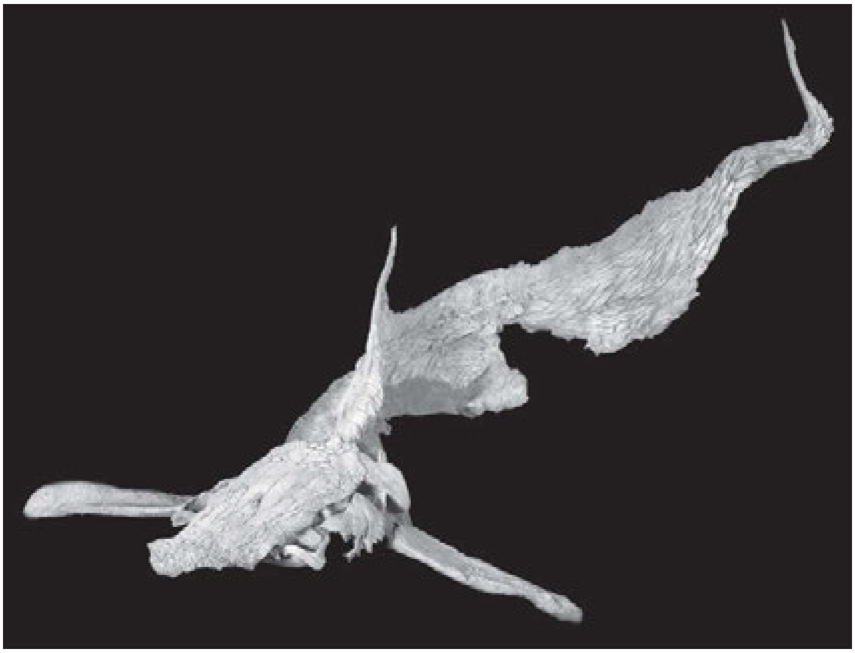

Figure 5.4. †*Priscosturion longipinnis* is the only well-preserved, articulated Sturgeon fossil with a relatively complete skeleton. This specimen (80 cm TL) is from the Upper Cretaceous Judith River Formation (about 78 mya), Montana (Grande & Hilton 2006, 2009; photograph by and used with permission of Eric Hilton).

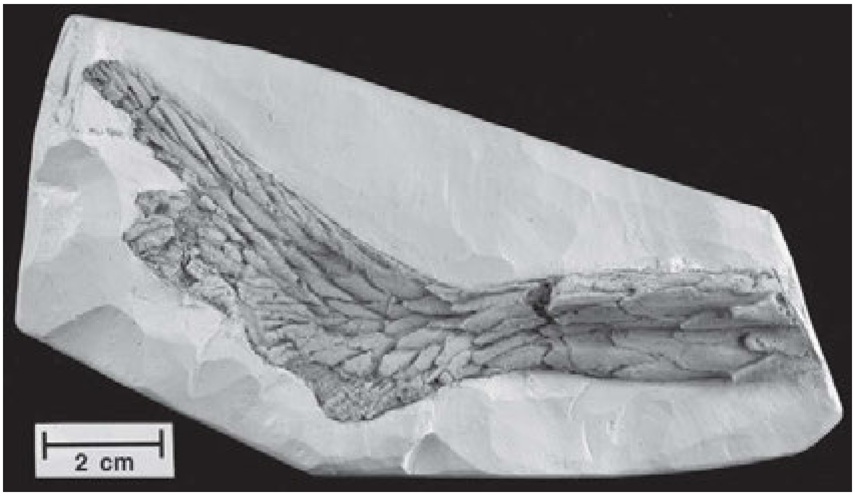

Figure 5.5. Tail region of †*Protoscaphirhynchus squamosus* from the Upper Cretaceous Hell Creek beds (about 65 mya), Montana (Hilton & Grande 2006; photograph by and used with permission of Eric Hilton).

Scaphirhynchus-like caudal fin region offers any unambiguous details. The apparent close relationship between †*P. squamosus* and *Scaphirhynchus* indicates that North American riverine Sturgeons have existed largely unchanged for ≥65 million years.

Both of these articulated fossil Sturgeon specimens, as well as a third as yet undescribed Sturgeon and a Paddlefish fossil, were discovered independently in abdominal areas of hadrosaurian (duck-billed) dinosaurs (Grande & Hilton 2006; Hilton & Grande 2006). Because these specimens are whole and hadrosaurs were plant eaters, the Sturgeons were not likely eaten. Instead, the dinosaur carcasses likely trapped the deceased Sturgeons and facilitated the rapid burial of these fishes by forming sediment traps in near-shore or river habitats (Grande & Hilton 2006).

Fossils of *Acipenser* are only represented by scutes and pectoral fin spines from ≤10 described fossil species (Wilimovsky 1956; Gardiner 1984; Birstein & DeSalle 1998; Choudhury & Dick 1998; Grande & Hilton 2006). In North America, these are represented by †*A. albertensis* and †*A. eruciferus* from the Late Cretaceous (about 99.6–65 mya), †*A. ornatus* from the Miocene (20–5 mya), and numerous other material only identified to genus from the Late Cretaceous to the Pliocene (5–2 mya). These fossils do not provide enough information to be useful in understanding relationships within Acipenseridae, and the validity of the described fossil species of *Acipenser* is questioned, given that the material cannot be readily distinguished from each other or from living Sturgeons (Findeis 1993, 1997; Bemis et al. 1997; Hilton & Bemis 1999; Hilton & Grande 2006). The fossils do indicate that *Acipenser* has existed for ≥65 million years.

The oldest fossil Sturgeon is †*Asiacipenser kotelnikovi* from the Middle Jurassic (about 176–161 mya) in Asia (Nessov et al. 1990). This is the only Sturgeon fossil that predates the Cretaceous, but some consider that the undiagnostic nature of the material (pieces and fragments) makes its assignment to Acipenseridae unreliable (Grande & Hilton 2006).

Most fossil Sturgeons, including the newly discovered †*P. longipinnis*, were recovered from deposits associated with freshwater and estuarine areas of coastal plains, the same environments used by present-day Sturgeons, indicating similar habitat for tens of millions of years (Choudhury & Dick 1998; Grande & Hilton 2006). These large riverine and near-shore habitats are high-energy environments that would facilitate the disarticulation of specimens before fossilization could occur, perhaps explaining the dearth of articulated Sturgeon fossil skeletons. The combination of fragmentary Sturgeon fossils and the overall conservative morphology of Sturgeons, including living species, make interpretation of the fossil record of Sturgeons difficult (Hilton & Grande 2006).

MORPHOLOGY

Sturgeons have an elongate, robust body that is subcylindrical in cross-section with the dorsal fin well back on the body behind the pelvic fins. The tail is heterocercal. Four conspicuous barbels are suspended in front of the highly protrusible, subterminal mouth. A rather large pair of nostrils with 20–30 olfactory lamellae is anterior to the small eyes. The body is covered with five rows of bony plates (scutes, one dorsal, two lateral, and two ventral), and bony platelets occur between the rows of scutes. Rhomboid scales are on the caudal peduncle, caudal fin, and abdomen (Fig. 5.6) and round-based scales on the internal surface of the pectoral girdle (Fig. 5.7). The four gill arches have relatively few gill rakers. Vertebral centra are lacking and adults lack teeth. The shoulder girdle forms a cardiac shield. Internally, the stomach has numerous pyloric appendages and the intestine a spiral valve. The gas bladder is simple with a connection to the gut (physostomous). The gonads are thick and elongate, extending along each side of the air bladder near the dorsal surface of the body cavity (Berg 1940; Vladykov & Greeley 1963; Nelson 1994; Mayden & Kuhajda 1996; Bemis et al. 1997; Findeis 1997; Hilton et al. 2011). Not all of these characters are derived (synapomorphies) for the order Acipenseriformes or family Acipenseridae (characters

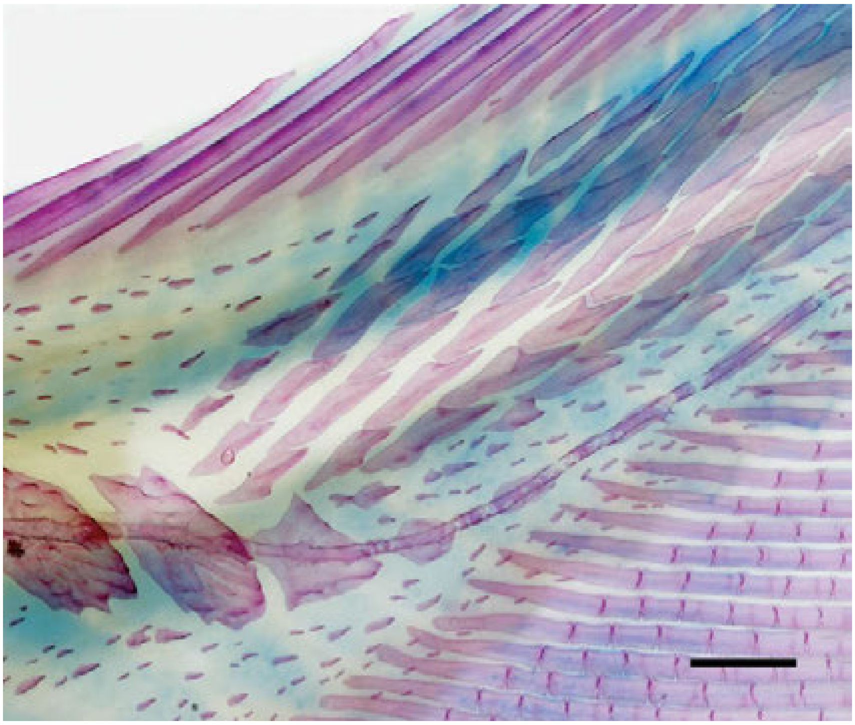

Figure 5.6. Cleared and stained caudal region of a Shortnose Sturgeon (*Acipenser brevirostrum*) showing angled vertical rows of rhomboid scale and small, scattered bony platelets. Scale bar = 2 mm (Hilton et al. 2011; photograph by and used with permission of Eric Hilton).

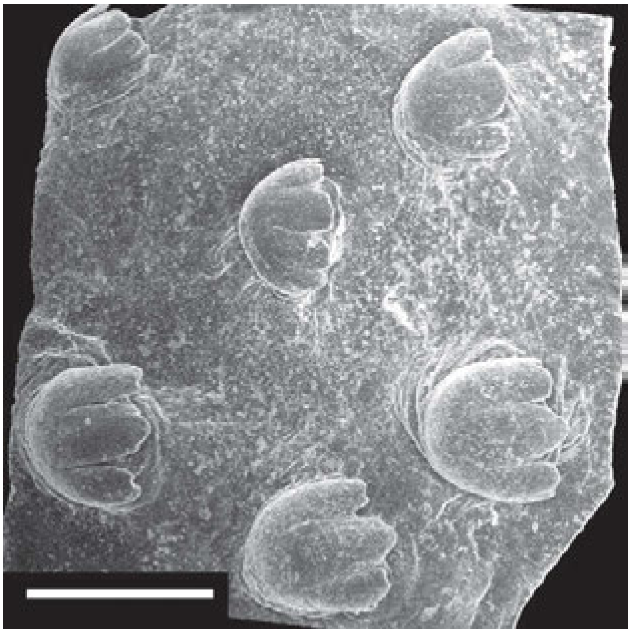

Figure 5.7. Scanning electron micrograph of small patch of skin on the internal surface of the pectoral girdle of a Shortnose Sturgeon (*Acipenser brevirostrum*) showing round-based scales. Scale bar = 0.25 mm (Hilton et al. 2011; photograph by and used with permission of Eric Hilton).

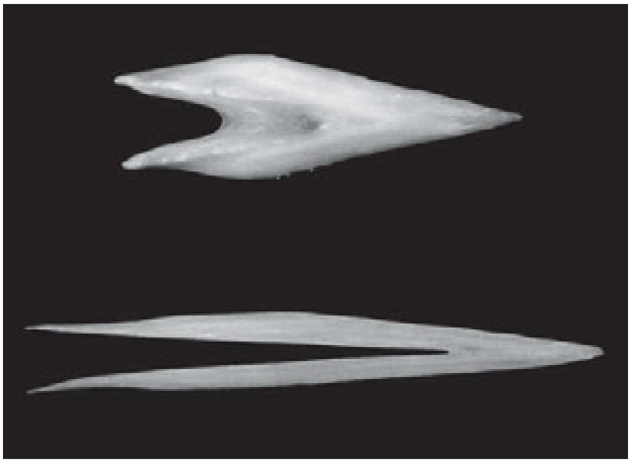

Figure 5.8. Dorsal caudal fulcra from a Shortnose Sturgeon (*Acipenser brevirostrum*) with anterior and more posterior fulcra on top and bottom, respectively (Hilton 2004; photograph by and used with permission of Eric Hilton).

unique to these taxa in Grande & Bemis 1991, 1996; Bemis et al. 1997; Findeis 1997; Hilton 2004; Grande & Hilton 2006; Hilton et al. 2011).

Ancient Body Plan

The basic body plan of living Sturgeons generally reflects that found in fossil Acipenseriformes from the Lower Jurassic (201.6–176 mya) and closely resembles fossil Sturgeons from the Late Cretaceous (78–65 mya) (Bemis et al. 1997). These relic characters include a subcylindrical body, a heterocercal tail; the endocranium greatly extended into a rostrum; reduced ossification of the endoskeleton and a persistent notochord; the head covered with bony plates separated by prominent sutures; a subterminal, protrusable mouth in which the upper jaw does not articulate with the cranium and the jaws are suspended from a mobile hyoid arch; the loss of the maxillary and premaxillary bones; no opercle; the subopercle, supported by a reduced number of branchiostegal rays (one to three), acts as the gill cover; fin rays more numerous than their basal supporting elements; novel scales, including median predorsal, preanal, and precaudal scales (fulcra) (Fig. 5.8); and a stout spine along the leading edge of the pectoral fin made of rays encased in a dermal bone sheath (Vladykov & Greeley 1963; Grande & Bemis 1991; Bemis et al. 1997; Findeis 1997; Grande et al. 2002). The endoskeletal elements of the pectoral fins of Sturgeons (and Paddlefishes) have elements homologous to both the fin radials of teleosts and the limb bones of tetrapods (Davis et al. 2004).

Benthic Cruisers

Although North American Sturgeons have morphological specializations for close interactions with the bottoms of rivers, lakes, estuaries, and oceans (see next three paragraphs), they lack extreme modifications such as flattened bodies, extensive camouflage, and stationary lifestyles. Many aspects of Sturgeon morphology reflect an active benthic lifestyle termed “benthic cruising” (Findeis 1997), representing the ecological guild supra-benthos cruisers (Vecsei & Peterson 2004). Distinct adaptations for benthic cruising include the lack of articulation of the upper jaw with the cranium, the subterminal placement of the mouth, and a novel jaw protrusion mechanism that allows for jaw projection toward the benthos with an accompanying suction to facilitate the capture of prey items (Findeis 1997; Carroll & Wainwright 2003; Miller 2004). A novel palatal complex shears across a tongue pad (with biting ridges) that grips prey as the upper jaw is projected and retracted as ingested substrate is sieved through. In Sturgeons that prey on smaller items (e.g., aquatic insects), gill rakers are branched and flattened to assist in prey retention (Findeis 1997; Vasil’eva 1999). Normal gill ventilation in Sturgeons is accomplished with a buccal pump, where water is pumped into the mouth and out of the ventral opening of the subopercle. An accessory flow system is used when the mouth is blocked with prey and substrate during feeding; water is brought into the opercular chamber through the dorsal edge of the gill cover. Species of *Acipenser* possess a spiracle, a vestigial gill opening with a canal that leads to the opercular cavity. A small gill (pseudobranch) lines the internal opening of the spiracle canal, but these structures play no role in gill ventilation (Burggren 1978).

All Sturgeons possess structures on the ventral surface of the rostrum called ampullary organs that likely use electroreception to detect the weak electrical fields emitted by prey items (Teeter et al. 1980; New & Bodznick 1985; Miller 2004). In *Scaphirhynchus* ampullary organs are found in clusters of 20 (on average) distributed on the dorsal, lateral, and ventral surfaces of the head and on the subopercle, with the largest number covering the entire ventral surface of the rostrum except for a small anterior midline oval area (Fig. 5.9). About 1,300 ampullary clusters were counted in an individual, indicating a total of >20,000 ampullary organs present (Northcutt 1986). Although the anterior lateral-line nerve innervates both ampullary organs and mechanoreceptive neuromasts of the cephalic lateral-line system, a clear division exists between these sensory systems in the hindbrain of Sturgeons (and the Paddlefish) (New & Bodznick 1985). Because the sensory epithelium and function of the ampullary organs of Sturgeons is similar to Lorenzinian ampullae found in elasmobranchs, the electrosensory system in Acipenseroidei likely is derived from a common ancestor shared with cartilaginous fishes (New & Bodznick 1985; Northcutt 1986). The overall flattening of the head of Sturgeons may be associated with the expansion of these electroreception ampullary fields and with the ventral placement of the mouth. The rostrum of *Acipenser* is subconical but *Scaphirhynchus*, the most benthic genus of North American Sturgeons, has an extremely flattened rostrum along with a flatter body and a flattened and completely armored caudal peduncle, all modifications reflecting a close association with river bottoms (Findeis 1997). Juveniles of *Acipenser* are more benthic than adults and correspondingly have more dermal armoring (Findeis 1997).

Other specialized rostral structures include barbels and lip papillae that have chemoreceptors (taste buds) to detect benthic prey (Bemis et al. 1997; Kasumyan 1999, 2002). Some species of *Scaphirhynchus* have highly fringed barbels and fringed papillae on lobes on their lips to presumably increase detection of prey items (Miller 2004).

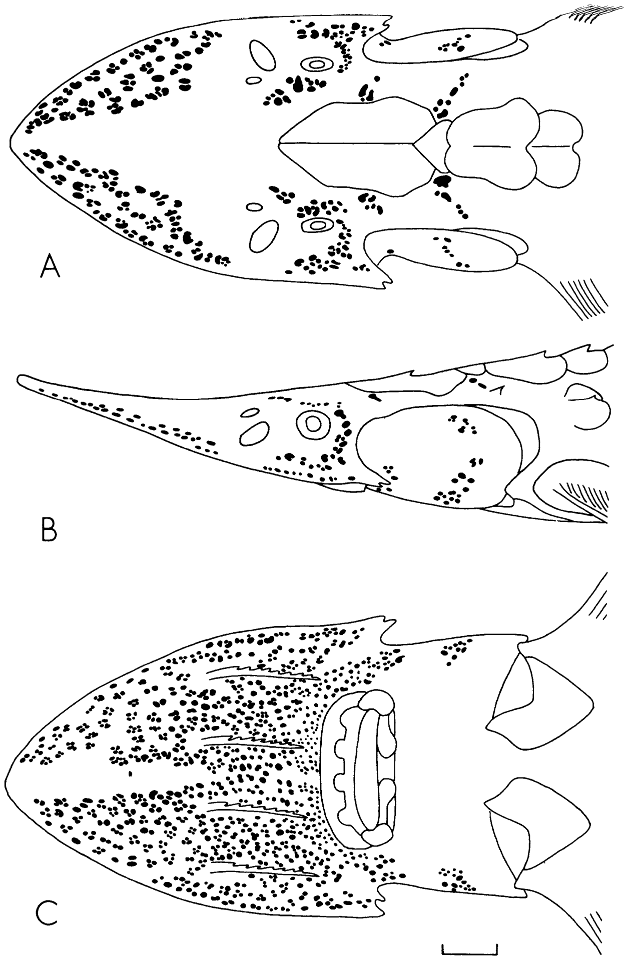

Figure 5.9. Drawing of the head of *Scaphirhynchus* stained with methylene blue showing ampullary organs in clusters on the dorsal, lateral, and ventral surfaces of the head and on the subopercle. Scale bar = 1 cm (Northcutt 1986; illustrated by and used with permission of Glenn Northcutt).

Sturgeons also have a lateral-line canal system on the underside of the rostrum, as well as on the lateral and dorso-lateral surface of the head. The lateral line extends concealed under the lateral row of scutes onto the upper lobe of the heterocercal caudal fin (Forbes & Richardson 1920; Norris 1924; Hilton 2004).

Species of *Scaphirhynchus* possess a long caudal filament (circus) representing an extension of the notochord. The caudal filament likely has some sensory function because it has nerves and a lateral line along its length (Weisel 1978); this structure is often missing or incomplete in adults (Bailey & Cross 1954). In *Scaphirhynchus* the lower lobe of the deeply forked heterocercal caudal fin is reduced to allow for tail movement in close proximity to the bottom (Findeis 1997; Vecsei & Peterson 2004).

Other modifications for a benthic lifestyle include the pectoral fin spines that some species of *Scaphirhynchus* use to walk along the substrate and an abdominal area protected with heavy scales (Findeis 1997). Species of *Scaphirhynchus* also possess varying degrees of head spines, including preorbital, parietal, post-temporal, and tabular spines with some species having recurved spines on the dorsal tip of the rostrum (Bailey & Cross 1954; Mayden & Kuhajda 1996; Vecsei & Peterson 2004).

Swimming

Sturgeons are classified as benthic cruisers, swimming horizontally just above the substrate in search of food (Findeis 1997; Vecsei & Peterson 2004). The classic model explaining how fishes with heterocercal tails such as Sharks and Sturgeons maintain a horizontal cruising plane postulates that the lift and movement produced by the heterocercal tail would pitch the head ventrally if not countered by lift produced by the pectoral fins. But a new model based on three-dimensional coordinate data from tank observations on juvenile White Sturgeons proposes that a horizontal cruising plane is maintained with lift from the dorsally angled ventral body surface both anterior and posterior to the body center that is countered with the negative buoyancy of the Sturgeon at the body center (center of mass); heterocercal tail oscillations only generate forward thrust and the pectoral fins do not generate lift. But the posterior portions of the pectoral fins are actively moved ventrally or dorsally to induce rising or sinking respectively by reorienting the head and body in the flow (Fig. 5.10). In current speed of 0.5 body length/s, Sturgeons have a positive body tilt of 20 degrees. In current speed of 1.0 body length/s Sturgeons have a positive body tilt of 8 degrees (Wilga & Lauder 1999).

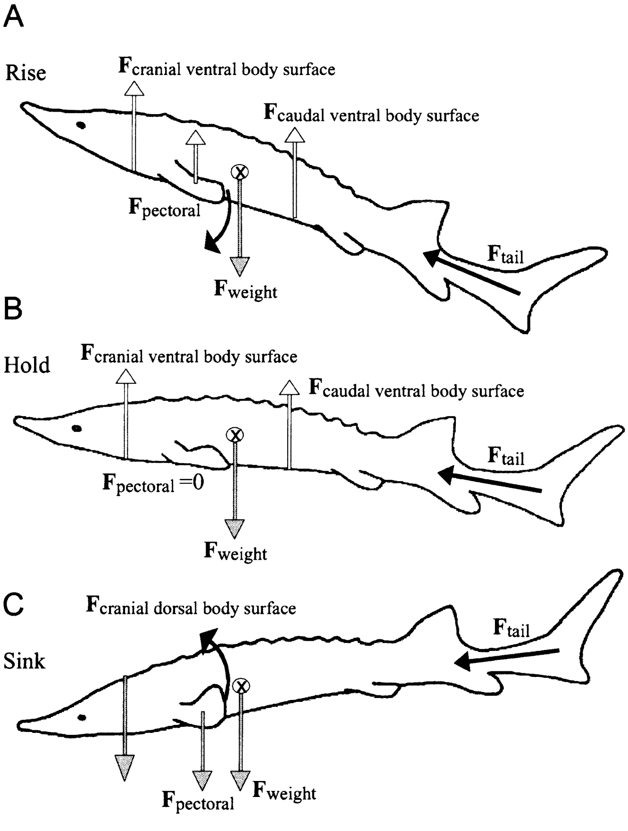
A
Rise
$F_{\text{cranial ventral body surface}}$
$F_{\text{caudal ventral body surface}}$
F_{pectoral}
F_{tail}
F_{weight}
B
Hold
$F_{\text{cranial ventral body surface}}$
$F_{\text{caudal ventral body surface}}$
F_{tail}
$F_{\text{pectoral}}=0$
F_{weight}
C
$F_{\text{cranial dorsal body surface}}$
F_{tail}
Sink
F_{pectoral}
F_{weight}

Figure 5.10. Diagram of vertical force balance on swimming Sturgeon with X as the center of mass and vertical arrows indicating force exerted by the fish as the posterior portions of the pectoral fins are actively moved ventrally or dorsally to induce rising or sinking, respectively, by reorienting the head and body in the flow. The tail arrow indicates forward force (Wilga & Lauder 1999; reproduced with permission of The Journal of Experimental Biology).

Size

Sturgeons are the largest fishes found in fresh water (Tables 5.1 and 5.2). *Acipenser* contains the largest North American Sturgeons, ranging from the giant White Sturgeon that can reach 6.1 m TL (20 feet) and weigh 816 kg (1,800 pounds), to the Shortnose Sturgeon that attains 1.4 m TL (4.6 feet) and 23 kg (51 pounds). The Pallid Sturgeon is the largest species of *Scaphirhynchus*, reaching a maximum size of 1.7 m TL (5.6 feet) and 45 kg (99 pounds); the Alabama Sturgeon is the smallest at 78 cm TL (2.5 feet) and 3 kg (6.6 pounds) (Williams & Clemmer 1991; Cech & Doroshov 2004).

Female Sturgeons attain larger sizes (and greater ages) compared with males, but otherwise show no obvious external sexual dimorphism except when they are ripe. Before spawning, females have swollen abdomens full of ripe eggs, and males are more elongate, but substantial overlap can occur between the sexes (Vladykov & Greeley 1963; Noakes et al. 1999; Kennedy et al. 2006; Van Eenennaam et al. 2006). Reliable minimally invasive techniques to determine the sex of Sturgeons and reproductive readiness include, in order of increasing accuracy, field ultrasound, endoscopy, and blood plasma assays (Colombo et al. 2004; Wildhaber et al. 2007; Craig et al. 2009; Divers et al. 2009; Heise et al. 2009).

Early Life Stages

Sturgeons progress through large morphological changes in early life stages. Immediately upon hatching larvae have yolk sacs and are classified as proto-larvae that lack

Table 5.1. Life history attributes for five species of Sturgeons in the genus *Acipenser* in North America.

Life History Attribute	***Acipenser* (five species, one with two subspecies)**	**References**
Strictly freshwater	Anadromous (two), semi-anadromous (two), potamodromous (one)	Boreman 1997; Wilson & McKinley 2004
Maximum size recorded in length and weight	1.43 m TL (4.7 feet) and 23 kg (51 pounds) to 6.1 TL m (20 feet) and 816 kg (1,800 pounds)	Cech & Doroshov 2004
Maximum age	60–152 years	Cech & Doroshov 2004
Age at first reproduction	Males 2–12 years and females 4–18 years to males 15–20 years and females 22–33 years	Dadswell 1979; Cochnauer et al. 1985; Smith 1985; Kynard 1997; McLeod et al. 1999; Van Eenennaam et al. 2006
Iteroparous or semelparous	Iteroparous	Boreman 1997; Billard & Lecointre 2001
Fecundity estimates (ovarian counts)	27,000–208,000 to 400,000–2.6 million	Dadswell 1979; DeVore et al. 1995; Boreman 1997; Van Eenennaam & Doroshov 1998; Van Eenennaam et al. 2001, 2006; Bruch & Binkowski 2002; Bruch et al. 2006
Mature egg diameter	1.74–2.49 mm (0.07–0.10 inch), average 2.21 mm (0.09 inch), to 4.04–4.66 mm (0.16–0.18 inch), average 4.33 (0.17 inch)	Scott & Crossman 1973; Dadswell 1979; Cherr & Clark 1985; Parauka et al. 1991; Van Eenennaam et al. 1996, 2006; Van Eenennaan & Doroshov 1998; Bruch et al. 2006
Egg deposition sites	Hard or rocky substrate	Parsley et al. 1993; Sulak & Clugston 1999; Bruch & Binkowski 2002
Clutch size	957–1,444 eggs/spawning bout (*A. fulvescens*)	Bruch & Binkowski 2002
Range of spawning dates and temperatures	March–July; 8.8–23°C (47.8–73.4°F)	Dadswell 1979; Parsley et al. 1993; Sulak & Clugston 1999; Fox et al. 2000; Bruch & Binkowski 2002; Erickson et al. 2002; Perrin et al. 2003; Wilson & McKinley 2004; Van Eenennaam et al. 2005, 2006
Habitat of spawning sites; average water depth	Hard or rocky substrate; 0.5–4.7 m (1.6–15.4 feet) to 2–27 m (6.6–88.6 feet)	Parsley et al. 1993; Fox et al. 2000; Bruch & Binkowski 2002; Perrin et al. 2003; Wilson & McKinley 2004
Incubation period; larval type at hatching	2.3–2.5 days at 22.2–23.3°C (72–73.9°F) to 8–14 days at 10–14°C (50–57.2°F); all species protolarvae at hatching	Smith et al. 1980; Buckley & Kynard 1981; Kempinger 1988; Parauka et al. 1991; Richmond & Kynard 1995; Kynard 1997; Van Eenennaam et al. 2001; Deng et al. 2002
Mean size at hatching	Average 7.1 mm (0.28 inch) TL to 12.6–15 mm (0.50–0.59 inch) TL	Smith et al. 1980; Buckley & Kynard 1981; Richmond & Kynard 1995; Kynard 1997; Bardi et al. 1998; Van Eenennaam et al. 2001; Deng et al. 2002; Snyder 2002
Parental care	None	Bruch & Binkowski 2002
Major dietary items	Nematodes, oligochaetes, amphipods, aquatic insects, mollusks, crayfishes, and fishes in fresh water; mysids, copepods, and fishes in brackish and marine waters	Hatin et al. 2002; Jackson et al. 2002; Wilson & McKinley 2004
General year-round habitat	Anadromous adults in near-shore marine waters and semi-anadromous adults in estuaries in brackish water, except when spawning; potamodromous and landlocked Sturgeon in large rivers or lakes with adults occasionally found in brackish water	Wilson & McKinley 2004
Migratory or diadromous	Migratory (one) and diadromous (four)	Erickson et al. 2002; Wilson & McKinley 2004
Imperilment status	All species except one (*A. fulvescens*) with a distinct population or all populations federally Endangered or Threatened	Auer 2004; Wilson & McKinley 2004; NMFS 2006, 2010ab

Table 5.2. Life history attributes for three species in the genus *Scaphirhynchus* (—, not applicable).

Life History Attribute	***Scaphirhynchus* (three species)**	**References**
Strictly freshwater	Potamodromous	Boreman 1997; Wilson & McKinley 2004
Maximum size recorded in length and weight	0.78 m TL (2.5 feet) and 3 kg (6.6 pounds) to 1.68 m TL (5.5 feet) and 45 kg (99 pounds)	Williams & Clemmer 1991; Cech & Doroshov 2004
Maximum age	41–43 years	Keenlyne & Jenkins 1993; Everett et al. 2003
Age at first reproduction	Males, ≥5 years; females, 6–12 to 15–20 years	Keenlyne & Jenkins 1993; Keenlyne 1997; Kennedy et al. 2006
Iteroparous or semelparous	Iteroparous	Boreman 1997; Billard & Lecointre 2001
Fecundity estimates (ovarian counts)	7,069–65,490 to 170,000	Keenlyne et al. 1992; Kennedy et al. 2006
Mature egg diameter	2.0–2.5 mm (0.08–0.10 inch) to an average of 2.6 mm (0.10 inch)	Keenlyne et al. 1992; Kennedy et al. 2006; Bryan et al. 2007
Egg deposition sites	Hard or rocky substrate	Parsley et al. 1993; Sulak & Clugston 1999; Bruch & Binkowski 2002
Clutch size	Unknown	—
Range of spawning dates and temperatures	February–July; 16.9–21.2°C (62.4–70.2°F)	Keenlyne & Jenkins 1993; Mayden & Kuhajda 1997a; Wilson & McKinley 2004
Habitat of spawning sites; average water depth	Unknown	—
Incubation period; larval type at hatching	5 days at 20°C (68°F), 5–14 days at 14°C (57.2°F), 7–13 days at 13–16.5°C (55.4–61.7°F); all species proto-larvae at hatching	Snyder 2002; Colombo et al. 2007b
Mean size at hatching	7–9 mm (0.28–0.35 inch) TL	Snyder 2002
Parental care	None	Bruch & Binkowski 2002
Major dietary items	Aquatic insects, snails, mussels, fish eggs, and occasionally fishes, switching to mostly piscivorous diet as juvenile and adult in *S. albus*	Carlson et al. 1985; Gerrity et al. 2006; Hoover et al. 2007; Keevin et al. 2007; Rapp et al. 2011
General year-round habitat	Main channel, borders, or pools downstream of sand bars or wing dikes in large rivers in areas of high to moderate flows over stable substrate	Keenlyne 1997; Mayden & Kuhajda 1997a; Wilson & McKinley 2004
Migratory or diadromous	Migratory	Mayden & Kuhajda 1997a; Wilson & McKinley 2004
Imperilment status	Two species federally Endangered and one species with a distinct population federally Threatened	Auer 2004; Wilson & McKinley 2004; USFWS 2010a

obvious Sturgeon features. As proto-larvae grow they completely absorb their yolk sacs and develop a subterminal mouth and barbels shortly before active feeding (6–10 days post-hatch). Mesolarvae develop median fin elements, an elongated rostrum, teeth (lost as juveniles) (Fig. 5.11), and rows of scutes, and resemble miniature adults at the end of this stage (around 31–45 days post-hatch). Members of *Acipenser* metamorphose into juveniles at this point and are from 31 to 94 mm TL. In *Scaphirhynchus*, individuals pass into a third larval stage (metalarvae) at a size of 55–90 mm TL, where all fin rays are present but an anal fin fold persists, and this fold is present in specimens ≥200 mm TL (Bath et al. 1981; Richmond & Kynard 1995; Deng et al. 2002; Snyder 2002; Colombo et al. 2007b). Species identification of proto-larvae within genera, although difficult, can be realized (Deng et al. 2002; Synder 2002).

Paedomorphosis and Peramorphosis

Conventional views invoke paedomorphosis (juvenile characters expressed in adults) to explain the secondary de-ossification of the largely cartilaginous skeleton and the loss of dermal elements in Sturgeons, and accept paedomorphosis as one of the driving forces in Sturgeon evolution (Traquair 1877; Goodrich 1909; Gregory 1933; Yakovlev 1977; Vecsei & Peterson 2004). Rare documented direct evidence for paedomorphosis includes delayed ossification of skeletal elements in adult Shortnose Sturgeons (Bemis et al. 1997). This, however, is not conclusive (Hilton & Bemis 1999), and no studies support the role of delayed ossification in evolution of Sturgeons (Bemis et al. 1997; Findeis 1997). In fact, phylogenies of acipenserids based on osteology demonstrate that additions and enlargement in skeletal elements and an increase in scalation occurred within Sturgeons at all phylogenetic nodes, which suggests that peramorphosis (addition of new or enlargement of existing structures compared with outgroups), rather than paedomorphosis, has played a central role in Sturgeon evolution (Findeis 1997).

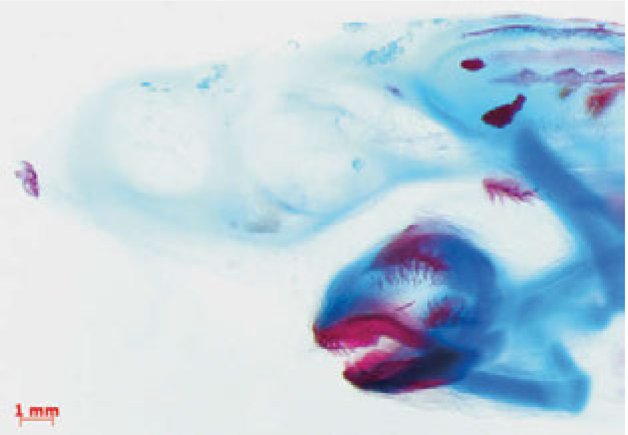

Figure 5.11. White Sturgeon, *Acipenser transmontanus*, larva 12 days post-hatch (22.28 mm TL) showing teeth that are lost in juveniles and adults (photograph by and used with permission of Katie May Laumann).

GENETICS

Karyology

Sturgeons possess a karyotype with large numbers of chromosomes. Species are separable into classes of about 120, 250, and perhaps 500 chromosomes (Birstein et al. 1997b; Fontana 2002). The latter group is tentative because it is based on DNA content and not on actual number of chromosomes (Blacklidge & Bidwell 1993). Up to half of these chromosomes are small microchromosomes with the remaining consisting of larger metacentric and submetacentric macrochromosomes. A diploid ancestor to all Acipenseriformes likely had 60 chromosomes, and a gene duplication event created a tetraploid (4n) ancestor (Birstein et al. 1997b; Ludwig et al. 2001). Some consider extant Sturgeons as tetraploid, octoploid (8n), and perhaps 16n-ploid species (Birstein et al. 1997b; Kim et al. 2001), which is the highest level of polyploidy in fishes (Vasil'ev 1999). Others treat Sturgeons with 120 chromosomes as functional diploids and those with 250 chromosomes as tetraploids (Ludwig et al. 2001; Fontana 2002; Fontana et al. 2004). The chromosome number for North American Sturgeons is known in 5 species with the Shovelnose Sturgeon and Atlantic Sturgeon in the 120 chromosome group, and the Lake Sturgeon, Green Sturgeon, and White Sturgeon in the 250 chromosome group. No direct data are available for the other species of *Scaphirhynchus* or Shortnose Sturgeon, but the genome size of the Shortnose Sturgeon suggests it may have 360 or 500 chromosomes (Birstein et al. 1997b; Fontana 2002; Fontana et al. 2004). Phylogenetic relationships and divergence times based on molecular data indicate that several genome duplication events created the diverse polyploidy in North American Sturgeons, ranging from <35.4 to 70 mya (Peng et al. 2007). Microsatellite DNA studies revealed complex modes of inheritance in North American species possessing 250 chromosomes, including patterns suggesting disomic, tetrasomic, and perhaps octosomic systems in the White Sturgeon (Rodzen & May 2002). These contrast with patterns in the Lake Sturgeon that suggest this species is evolving from tetrasomy to disomy (McQuown et al. 2002).

Polyploidy in Sturgeons is the likely origin of multiple nuclear gene sequence variants within individuals. Intra-individual variation of the 18S rRNA gene is present in all genera of Sturgeons, and all species examined to date, including the eight North American species of Sturgeon. This phenomenon is not known in any other vertebrate, including the Paddlefish, because concerted evolution is believed to homogenize any multiple copies of rDNA within individuals (Krieger & Fuerst 2002a; Krieger et al. 2006). A more common form of genetic variation within an individual's genome is heteroplasmy, where the mitochondrial genome has length variants via repeat units. Heteroplasmy is present in all North American species of *Acipenser* except the Atlantic Sturgeon, but no species of *Scaphirhynchus* are heteroplasmic (Ludwig et al. 2000).

Low Genetic Divergence

Another unique aspect of Sturgeons is the overall low genetic diversity at commonly used molecular markers. One hypothesis for low genetic differentiation is recent speciation of extant species of Sturgeons in the Late Tertiary or Pleistocene (Choudhury & Dick 1998; Campton et al.

2000). A second explanation is hybridization between sympatric species (Campton et al. 2000), which occurs within or between all genera of Sturgeons (Birstein et al. 1997b). But most research points to an extremely slow rate of molecular evolution for all Sturgeons as the factor producing a lack of variation in genetic markers, possibly stemming from long generation times, low metabolic rates, and slow rates of concerted evolution (de la Herrán et al. 2001; Krieger & Fuerst 2002b, 2009; Robles et al. 2004). Another explanation involves the evolutionary pathway of polyploidization via complex hybridization in the diversification of Sturgeons as the source of reduced genetic differences between taxa (Robles et al. 2005) (see phylogenetic relationships section). In general, less species- and population-level resolution is obtained from sequencing the mitochondrial genome relative to examining nuclear loci (Wirgin et al. 1997; King et al. 2001; Robinson & Ferguson 2004), but the discovery of multiple copies of nuclear gene sequences within individual Sturgeons indicates that patterns of sequence divergence may not necessarily reflect patterns of species divergence (Krieger & Fuerst 2002a; Krieger et al. 2006).

Lack of Vouchering

An additional confounding factor in genetic research of Sturgeons is the overall lack of vouchering protocols associated with the harvesting of tissues, which is of greatest concern when sympatric congeneric species are involved. Specimens are rarely retained, and detailed data appropriate for species identification (measurements and photos) are often not recorded, therefore verification of identification is not possible. This is especially a concern for juveniles and subadults for which allometric growth can delay the development of diagnosable morphological characters (Kuhajda et al. 2007).

Identification of Species, Species Boundaries, and Hybrids

The complex genetic structures of Sturgeons coupled with slow rates of change at commonly used markers are challenging for molecular research, but genetics are a useful tool in examining the relationships of species, genera, and subfamilies within Acipenseridae (see phylogenetic relationships section). Genetic data also are used to examine species boundaries and hybridization as well as species identification in the caviar trade. The two subspecies of *Acipenser oxyrinchus* (Atlantic Sturgeon, *A. o. oxyrinchus*, and Gulf Sturgeon, *A. o. desotoi*) are similar morphologically (Wooley 1985), but mitochondrial and microsatellite DNA studies have supported their distinctiveness (Ong et al. 1996; Krieger et al. 2000; King et al. 2001). Species of *Scaphirhynchus* inhabit commercially important large river ecosystems, and their endangered status has spurred questions regarding their species status (Mayden & Kuhajda 1996, 1997ab); there also are concerns that the two *Scaphirhynchus* species sympatric in the Mississippi River Basin (Pallid and Shovelnose Sturgeon) hybridize (Carlson et al. 1985; USFWS 1993). Mitochondrial DNA and microsatellite loci studies supported the specific status of all three species of *Scaphirhynchus*. These same techniques indicated the presence of introgressive hybridization between the endangered Pallid Sturgeon and the relatively common Shovelnose Sturgeon across most of the Pallid Sturgeon's range. The hybridization may be natural rather than a product of human-induced habitat changes in the Missouri and Mississippi Rivers. This raises concern over the genetic integrity of brood stock for the Pallid Sturgeon propagation and stocking recovery program (Campton et al. 2000; Allendorf et al. 2001; Simons et al. 2001; Tranah et al. 2001a, 2004; Ray et al. 2007; Schrey & Heist 2007; Schrey et al. 2007, 2011). For other genera, mitochondrial DNA sequences and amplified fragment length polymorphism using nuclear loci from eggs and flesh are useful in differentiating *Acipenser* and *Huso* and some species of *Acipenser* (DeSalle & Birstein 1996; Birstein et al. 1999; Wolf et al. 1999; Congiu et al. 2002), potentially giving law enforcement agencies a forensic tool to monitor trade of Sturgeon commercial products.

Population Genetics

As Sturgeon populations continue to decline, stocking hatchery-raised specimens will become more prevalent, and intraspecific genetic variation in natural populations must be identified and maintained (Wirgin et al. 1997; Fontana et al. 2001). Within *Acipenser*, adults of the Western Atlantic species (Shortnose Sturgeon, Atlantic Sturgeon, and Gulf Sturgeon) demonstrate fidelity to rivers where they were spawned (natal fidelity). Mitochondrial DNA sequences, and on a finer scale microsatellite loci, reflect this river fidelity within these species (Wirgin et al. 1997, 2000, 2002, 2005; Walsh et al. 2001; King et al. 2001; Grunwald et al. 2002; Quattro et al. 2002; Waldman et al. 2002; Dugo et al. 2004). Based in part on genetic data, Atlantic Sturgeon populations in the United States were recognized as five Distinct Population Segments (DPS) with each one proposed for federal protection (King et al. 2001; NMFS 2010ab). A study analyzing samples from more populations and attempting to obtain known river-of-origin samples determined that all riverine populations are genetically distinct and at least nine DPS should be recognized and protected (Grunwald et al. 2008). In West Coast *Acipenser*, these molecular techniques identified distinct management units of the White Sturgeon in the Frazer River, British Columbia (Smith et al. 2002a). Similarly, Green Sturgeons along the Pacific Coast are recognized as two DPS with the southern DPS protected as federally threatened (Israel et al. 2004; NMFS 2006; Adams et al. 2007). In the Lake Sturgeon, early molecular work failed to detect distinct populations and only found differences at the drainage level (Ferguson et al. 1993; Guénette et al. 1993; Ferguson & Duckworth 1997), but subsequent research demonstrated significant levels of population structure in the Great Lakes, again also attributable to natal fidelity (McQuown et al. 2003; DeHaan et al. 2006). Within the Mississippi River basin, both Pallid Sturgeons and Shovelnose Sturgeons demonstrated differences in mitochondrial DNA and microsatellite loci between northern and southern populations (Campton et al. 2000; Tranah et al. 2001a). These molecular techniques also demonstrated depressed genetic diversity in the Shortnose Sturgeon within a river system potentially because of stocking programs (Quattro et al. 2002).

PHYSIOLOGY

For the Pallid Sturgeon, Alabama Sturgeon, and Green Sturgeon little data are available on physiology (or behavior, reproduction, and ecology). Many traits commonly attributed to these species in the literature are extrapolated from other species of North American Sturgeons. Here the focus is on metabolism, digestion, osmoregulation, salinity tolerance, temperature and oxygen requirements, vision, aspects of egg and sperm interaction, senescence, and behavioral responses to environmental extremes.

Metabolism

Sturgeons have a relatively low metabolic rate (Krieger & Fuerst 2002b), both during rest and periods of active swimming (Burggren 1978; Burggren & Randall 1978). Oxygen consumption and oxidative metabolism are 5.5 and 4 times lower, respectively, in Sturgeons compared with salmonids. Gill surface area relative to body mass is low compared with that of other fishes, again reflective of a low metabolic rate and likely linked to a benthic lifestyle (Burggren 1978; Burggren et al. 1979; Singer et al. 1990). The overall metabolism of Sturgeons and the Paddlefishes bridges the evolutionary gap between elasmobranchs and teleosts (Singer et al. 1990; Singer & Ballantyne 2004). Sturgeon lipid metabolism is intermediate between elasmobranch and teleost models. Sturgeons may be among the first fishes to mobilize and transport some plasma fatty acid. Sturgeons have low but detectable products from ketone body metabolism, which is a retained primitive feature of elasmobranchs that is absent from all teleosts (Singer et al. 1990). Sturgeons excrete ammonia across their gills, as do most teleosts, rather than excreting urea as do most elasmobranchs. Cortisol is the main stress steroid in Acipenseriformes and higher vertebrates. Likewise Sturgeons possess sex hormones similar to those found in teleosts. Preliminary studies indicate that the capacity to detoxify various compounds may be lower in Sturgeons compared with teleosts (Singer & Ballantyne 2004).

Digestion

Sturgeons are carnivores during all life stages, and their short digestive tract reflects that of a primitive carnivore. This includes a short esophagus, which transports food to a secretory forestomach where food is stored and chemical digestion is initiated. This is followed by a nonsecretory stomach (pylorus or gizzard) where food is mechanically broken down by the action of smooth muscle. Posterior to the stomach is a flat, triangular pyloric caecum attached to the upper intestine. Nutrient absorption occurs in these structures. The intestine continues as a spiral valve, where a spiral, corkscrew folding of tissue along the length of the structure increases the absorptive surface without increasing the length of the gut. Lymph nodes are abundant in the thickened margin of the spiral valve of Sturgeons, as well as in other organs, perhaps as a mechanism evolved as a defense against parasitic infection and other diseases. A short rectum leads to the vent (Buddington & Christofferson 1985; Fänge 1986).

Larval Sturgeons feed on zooplankton that have higher lipid content relative to the macroinvertebrates and fishes preyed on by juveniles and adults, and this is reflected in the high levels of digestive lipase in larvae compared with the high levels of trypsin and pepsin for protein digestion in older life stages (Singer et al. 1990). Some lipids are metabolized by later life stages and are made soluble by bile that is a combination of a more primitive bile alcohol and a more advanced bile acid. Peritoneal fat may be the main storage tissue for lipids, but lipids also occur at high levels in muscle tissue, especially red muscle, as well as in the liver and the digestive tract (Singer & Ballantyne 2004).

Osmoregulation

Sturgeons share some of the main features of osmotic regulation with teleosts, including gill epithelia with large numbers of chloride cells used for sodium and chloride secretion and kidneys used for calcium and potassium excretion (LeBreton & Beamish 1998). North American Sturgeons residing in brackish or marine waters have larger and more chloride cells compared with freshwater species. Unlike some other fishes, Sturgeons have few if any chloride cells associated with opercular membranes or pseudobranchs and spiracles (Altinok et al. 1998). Sturgeons maintain hypo-osmotic (low) plasma ion levels relative to sea water and hyperosmotic (high) levels relative to fresh water. Plasma ion regulation is slower in Sturgeons relative to teleosts, which may reflect the more stable environment of large-river systems inhabited by Sturgeons. Several amino acids are used as intracellular solutes for adaptation to sea water, and abrupt introduction to salt water causes additional amino acids to be used. Osmoregulation in high salinities and brackish water increases metabolism and decreases growth rates for some juvenile *Acipenser* relative to fresh water (Singer & Ballantyne 2004). No metabolic costs were evident for juvenile Green Sturgeons in either brackish or salt water relative to fresh water, but growth was affected in salt water for juveniles 100 and 170 days post-hatch (Allen & Cech 2007). The development of mechanisms that allow effective osmotic and ionic homeostasis in Sturgeons as they expanded from fresh water into the marine environment contributed greatly to the evolution of anadromy (Krayushkina 2006).

Salinity Tolerance

Anadromous species tolerate full seawater concentrations of 34 ppt as adults (Singer & Ballantyne 2004), but juveniles, especially small individuals, are less tolerant (McEnroe & Cech 1985; Altinok et al. 1998). Green Sturgeons successfully iono- and osomoregulate at age 1.5 years (75 cm TL, 29.5 inches, and 1.5 kg, 3.3 pounds), one of the youngest ages known for Sturgeons (Allen & Cech 2007). Shortnose Sturgeons and Atlantic Sturgeons 3–4 years old maintain a relatively constant serum osmolarity and ion concentration when transferred from fresh water to full salt water (Krayushkina 2006). One potamodromous species (Lake Sturgeon) can inhabit brackish water ≤15 ppt (LeBreton & Beamish 1998). Salt tolerance is poor for early life history stages of Sturgeons, even anadromous species. Larvae and age-0+ juveniles die at exposures of 5–10 ppt (Kynard & Horgan 2002a; Kynard & Parker 2004).

Temperature Capacity

North American Sturgeons occur over areas with a temperature variation of 30°C (54°F), and individuals (Gulf Sturgeon) can experience a 20°C (36°F) range (8.1–28.5°C, 46.6–83.3°F) over a year (Parkyn et al. 2007), but they prefer and perform optimally at temperatures <25°C (77°F) (Cech & Doroshov 2004). Spawning temperatures range from quite cool in the north (as low as 8–9°C, 46.4–48.2°F, for Shortnose Sturgeons, Lake Sturgeons, Green Sturgeons, and White Sturgeons) to fairly warm in the south (≤20–23°C, 68–73.4°F, for Gulf Sturgeons and Shovelnose Sturgeons) (McKinley et al. 1998; Fox et al. 2000; Wilson & McKinley 2004). Cool temperatures are required for proper egg development and ovulation for many species (10°C, 50°F, water temperature for the White Sturgeon) (Webb et al. 1999; Linares-Casenave et al. 2002). Embryo and larval development and survival is optimal for most species from 11 to 20°C (52–68°F) with a sharp decrease in normal development and survival above this range (Wang et al. 1985; Cech & Doroshov 2004; Van Eenennaam et al. 2005). Sturgeon yolk-sac larvae develop efficiently and successfully within this rather broad temperature range compared with other non-Sturgeon larvae that typically show decreased size as temperatures increase due to lower efficiency rates of yolk utilization. The consistently large size of Sturgeon larvae after absorption of their yolk sacs over a broad temperature range may be a competitive advantage through superior prey capture and predator avoidance (Hardy & Litvak 2004). Activity and growth of young Sturgeons increase with temperature, but the optimum is <25°C (77°F) (Cech & Doroshov 2004), with mortality of age-0 *Scaphirhynchus* spp. increasing when temperatures are >28°C (82°F) in the Mississippi River (Phelps et al. 2010b). As with many fishes, Sturgeons are more susceptible to low oxygen levels at higher temperatures (Secor & Gunderson 1998).

Oxygen Requirements

Because of their benthic lifestyle, Sturgeons can come in contact with areas of low levels of dissolved oxygen (hypoxia), and they are less tolerant of hypoxia than many other fishes (Secor & Gunderson 1998; Niklitschek & Secor 2005). Physiological and metabolic responses can vary. Some Sturgeons may be oxygen regulators, adjusting ventilation rates to compensate for lower oxygen levels and maintaining a constant respiration rate with a corresponding consistent aerobic metabolism. But most species of Sturgeons are oxygen conformers, showing a decline in respiration rates with a corresponding reduction in activity, metabolic rate, and aerobic metabolism when oxygen drops below ambient levels (Singer & Ballantyne 2004; Burggren & Randall 1978). Oxygen conformity was demonstrated in the White Sturgeon and Atlantic Sturgeon, where decreased activity decreased oxygen demand and allowed survival until oxygen levels improved (Singer et al. 1990; Crocker & Cech 1997; Secor & Gunderson 1998; Cech & Crocker 2002; Cech & Doroshov 2004). The White Sturgeon did not show any repayment of the oxygen debt, even after severe hypoxia, indicated by the lack of pH blood change that would be expected if anaerobic metabolism was used during reduced oxygen availability (Burggren & Randall 1978). In contrast, the Lake Sturgeon may use anaerobic metabolism during anoxic conditions and may produce alternative end-products to avoid lactate acidosis and thus survive (Singer et al. 1990). The White Sturgeon occupies waters with dissolved oxygen levels from 8 to 16 mg/l and avoids areas with ≤6 mg/l; low oxygen levels within a transition zone of a reservoir led to mortality (Sullivan et al. 2003). Young Sturgeons may be more sensitive to low oxygen levels; mortality of juvenile Atlantic Sturgeons and Shortnose Sturgeons occurred quickly at 3 mg/l and decreased growth was observed for the Atlantic Sturgeon at non-lethal levels (Secor & Gunderson 1998; Campbell & Goodman 2004). A single juvenile Atlantic Sturgeon was restricted to a small area in the Neuse River, North Carolina, upstream of the freshwater-saltwater interface that suffered from severely hypoxic bottom waters during summer and autumn. These conditions may have led to the extirpation of the Shortnose Sturgeon due to lack of suitable summer habitat in the river (Oakley & Hightower 2007). Laboratory studies indicate juvenile Green Sturgeons may tolerate moderate environmental hypoxia (Kaufman et al. 2007).

Swimming Performance

Sturgeons are positively rheotactic, orienting head-first into flowing water. Swimming performance into flow varies across sizes, populations, species, life stages, and temperatures. Sustained swimming (≥200 min) is used for migration and foraging and depends on aerobic metabolism. In the laboratory, small juvenile Pallid Sturgeons and White Sturgeons (13.0–16.8 cm FL, 5.1–6.6 inches, and 8.0–9.2 cm TL, 3.1–3.6 inches, respectively) maintained sustained swimming at lower water velocities of 10 and <30 cm/s (0.3 and <1 feet/s) compared with higher velocities of 25 and 40–50 cm/s (0.8 and 1.3–1.6 feet/s) maintained by large juveniles (17.0–20.5 cm FL, 6.7–8.1 inches, and 9.3–10 cm TL, 3.7–3.9 inches, respectively) (Adams et al. 1999a; Boysen & Hoover 2009). Prolonged swimming (0.5–200 min), which uses aerobic and anaerobic metabolism, is similar between lacustrine and riverine populations of juvenile Lake Sturgeons (35–70 cm/s, 1.1–2.3 feet/s) but differs between juvenile Pallid Sturgeons from Yellowstone River, North Dakota, and Atchafalaya River, Louisiana (15–40 versus 35–70 cm/s, 0.5–1.3 versus 1.1–2.3 feet/s, respectively) (Hoover et al. 2011a). Burst swimming is the highest speed attainable and is used for prey capture and predator avoidance but can only be maintained for a short time (<0.5 min) due to the accumulation of anaerobic metabolites. Small juvenile Pallid Sturgeons had burst speeds of 40–70 cm/s (1.3–2.3 feet/s) compared with 55–70 cm/s (1.8–2.3 feet/s) for large juveniles, and burst speeds of juvenile Shovelnose Sturgeons from the Yellowstone River (40–70 cm/s, 1.3–2.3 feet/s) were slower than those for Atchfalya River Shovelnose Sturgeons and juvenile Lake Sturgeons (>70 cm/s, >2.3 feet/s) (Adams et al. 1999a; Hoover et al. 2009a). Physiological changes in large juvenile Green Sturgeons (26.7–47.5 cm TL, 10.5–18.7 inches) as they transform to adapt to saltwater habitats may contribute to their slower 20-min critical swimming speed of 43.3 cm/s (1.4 feet/s) compared with 54.8 cm/s (1.8 feet/s) for small juveniles (12.0–26.6 cm TL, 4.7–10.5 inches) (Allen et al. 2006). Critical swimming speeds increased with temperature from 15.0 and 19.4 cm/s (0.5 and 0.6 feet/s) at 10°C (50°F) to 35.9 and 36.9 cm/s (1.2 feet/s) at 20°C (68°F) for 30-min critical speeds for juvenile Pallid Sturgeons and Shovelnose Sturgeons. In juvenile Green Sturgeons, 20-min critical swimming speeds increased from 45.1 cm/s (1.5 feet/s) at 19°C (66°F) to 51.8 cm/s (1.7 feet/s) at 24°C (75°F) (Adams et al. 2003b; Allen et al. 2006).

All Sturgeons have lower swimming performance relative to that of other fishes. *Scaphirhynchus* species rarely swim in the water column; instead they are typically skimming the substrate with their ventral body surface. Species of *Acipenser* and *Scaphirhynchus* use station-holding techniques in high flows in laboratory settings including hunkering (appression to the substrate involving angled pectoral fins), wedging (rostrum forced into crevices), and tail bracing (caudal fin pressed against a vertical surface). Those Sturgeons inhabiting high-velocity rivers likely use these strategies and seek low-velocity microhabitats while swimming (Adams et al. 1997, 1999b, 2003b; Allen et al. 2006; Hoover et al. 2011a).

Photoreceptors and Visual Pigments

Sturgeon retinas are dominated by rods that are sensitive photoreceptors responsible for vision in dim light, but they also possess substantial numbers of cones that allow for acute and color vision under bright-light conditions (Sillman & Dahlin 2004a). Sturgeon rods are morphologically similar to those of other vertebrates with an outer segment that has a large diameter and is cylindrical and long (Loew & Sillman 1993; Sillman et al. 1999, 2005). Shovelnose and Pallid Sturgeons possess a rare second narrow rod but all other fishes examined only have one type of rod (Sillman et al. 1999, 2005). An Asian species, the Stellate Sturgeon (*Acipenser stellatus*), may lack rods (Govardovskii & Zueva 1987). Sturgeon cones are robust and are found as a single cone with a globose inner segment from which a single tapering outer segment extends; other fishes typically have cones joined tightly together or have multiple outer segments (double, triple, or twin cones). Two morphotypes are present in Sturgeons: a common large cone that contains a colorless oil globule in the inner segment (Loew & Sillman 1993; Sillman et al. 1999) and a rare small cone that lacks an oil droplet (Govardovskii et al. 1992; Sillman et al. 2005). Some diurnal birds and turtles have oil globules in cones, but these are colored and assist with color vision. Only nocturnal vertebrates have colorless oil globules, and although the function is unknown, it is likely an adaptation for low-light conditions (Sillman & Dahlin 2004a). The densities of rods and cones are relatively low in Sturgeons, indicating that dim- and bright-light acuity and sensitivity is less than that for many other nocturnal vertebrates (Sillman & Dahlin 2004a). Specialized regions in the Sturgeon retina have only been observed for the Green Sturgeon (lacking in the Shovelnose Sturgeon and White Sturgeon), which possesses a horizontal visual streak that may aid in orientation (Sillman & Dahlin 2004b; Sillman et al. 2005).

Rods in Sturgeons possess a single mid-wavelength-sensitive pigment. All species have cones that are sensitive to long wavelengths and also have mid- or short-wavelength-sensitive pigments (Loew & Sillman 1993; Sillman et al. 1999, 2005). All visual pigments are porphyropsins (vitamin A_2 chromophore) that have longer wavelength absorptive maxima compared with rhodopsins (vitamin A_1 chromophore). Since fresh water is redder (i.e., longer wavelength visible light) than salt water, these pigments are perhaps an adaptation to Sturgeon spawning and rearing areas, which are located in fresh water even for semi-anadromous and anadromous species (Sillman et al. 1999, 2005). White Sturgeons possess only mid-wavelength-sensitive rods and cones (green light) in early larval stages. Long- and short-wavelength-sensitivity (red and blue light) does not appear in cones until week 10 and may correlate with individuals moving into an estuarine environment (Loew & Sillman 1993). Shovelnose Sturgeons that spend their entire lives in fresh water have all of their visual pigment complement throughout all life history stages (Sillman et al. 1999). The multiple pigments in cones of Sturgeons likely enhance contrast detection across a broad spectrum, which is advantageous in a light-limited environment and could be useful for orientation and detection of potential predators. Multiple pigments could even indicate the capability for color vision, but no study has specifically addressed this issue to date (Loew & Sillman 1993; Sillman & Dahlin 2004a; Sillman et al. 2005).

Hearing Abilities and the Inner Ear

Most teleost fishes have the pars inferior of the inner ear composed of two fluid-filled pouches, the sacculus and the lagena, each containing an otolith. In Sturgeons (and the Paddlefish) the pars inferior consists of just one fluid-filled pouch with no division between the otoliths. Sturgeons (and the Paddlefish) have hair cells aligned in both horizontal and vertical planes within the inner ear that provide evidence for directional hearing. Sturgeons (and the Paddlefish) are responsive to sounds ranging between 100 and 500 Hz and to the motion of water particles in a sound field rather than the sound pressure component (Lovell et al. 2005).

Egg, Sperm, and Environment Interactions

Upon contact with fresh water a Sturgeon egg releases a jelly coat that once hydrated becomes adhesive and allows the egg to adhere to the substrate. Calcium or magnesium ions must be present in sufficient concentration for jelly release and hydration. The pole of the egg without micropyles (vegetal pole) is more adhesive, leaving the micropyles facing upward for ease of fertilization. Unlike most fish eggs, Sturgeon eggs can remain viable for fertilization for hours after release. Sperm of most freshwater fishes does not possess an acrosome because the low ionic strength of fresh water can easily disrupt membranes and cause a premature acrosome reaction, but Sturgeon sperm exhibits prolonged motility (≥3 min), and acrosomes are stable even after 10 min in fresh water. In the laboratory, high levels of calcium (30 mM) or an elevated pH (9.5) can generate premature acrosome reactions (Cherr & Clark 1985), and calcium concentrations >18 mg/l in the lower Suwannee River Florida may contribute to the lack of spawning for Gulf Sturgeons even though suitable substrate and flow are available (Sulak & Clugston 1999). Egg fertilization commences with the acrosome reaction induced by a glycoprotein in the egg envelope that is species-specific in *Acipenser* and greatly reduces interspecific fertilization. The concentration of this glycoprotein on the egg surface may be too dilute to generate an acrosome reaction in the fast-flowing spawning environment of Sturgeons, but concentrations are sufficient within the egg micropyle for the acrosome reaction to occur. A fertilization filament (acrosome process) about 10 µm long is formed after the acrosome reaction that aids in fertilization, but the exact function of the filament is unknown. Because Sturgeon eggs possess multiple micropyles one would expect increased occurrence of polyspermy, but a cortisol reaction is initiated immediately after the sperm contacts the egg plasma membrane that seals the inner openings of all other micropyles. These physiological factors of the gametes are potential reproductive adaptations for Sturgeons to successfully broadcast spawn in a riverine environment (Cherr & Clark 1985; Psenicka et al. 2011).

Effects of Age and Interactions among Environmental Variables

Female Sturgeons may have decreased reproductive potential at an advanced age. Population viability analyses indicate that reproductive values decrease rapidly in female Pallid Sturgeons >35 years old (Bajer & Wildhaber 2007).

Behavioral Responses to Environmental Extremes

Sturgeons move to avoid unfavorable environmental conditions (Auer 1996). In stratified reservoirs, the White Sturgeon avoids transition zones where dissolved oxygen levels approach 6 mg/l (Sullivan et al. 2003), and under hypoxic conditions juvenile Atlantic Sturgeons will use the water surface to access more oxygen-rich water (Secor & Gunderson 1998).

Many Sturgeons live in northern areas with extreme cold and show low growth rates due to low average temperatures. But when growth is adjusted for by the average degree-days >5°C for April–October, Lake Sturgeon populations at higher latitudes actually have a higher growth rate compared with more southern populations (Power & McKinley 1997).

BEHAVIOR

Diel Periodicity

Sturgeons vary in their diel movements. Adult *Scaphirhynchus* do not display distinct diel movements, but Shovelnose Sturgeons tend to be more active at night compared with more daytime movement for Pallid Sturgeons. These behaviors are suggestive of temporal resource partitioning (Curtis et al. 1997; Bramblett & White 2001). Overall Shortnose Sturgeons do not demonstrate diel movement patterns, but individuals can occupy shoal habitat more often at night (Kynard et al. 2000). Some species show strong diel patterns with Gulf Sturgeons more active at night in all seasons except summer; spawning and downstream migration in autumn take place almost exclusively at night (Sulak & Clugston 1999; Wrege et al. 2011). Pronounced nocturnal behavior was observed in captive Green Sturgeons (Lankford et al. 2003), and Green Sturgeons were more active and occupied shallower depths at night in marine habitats (Erickson & Hightower 2007). In drift migration of early life history stages, activity differences occur within genera and species. Feeding larvae are diurnal in the Pallid Sturgeon but nocturnal in the Shovelnose Sturgeon, which may optimize larval migration and feeding for each species (Kynard et al. 2002a). In Atlantic Sturgeon larvae start as nocturnal migrators then switch to both nocturnal and diurnal migration (Kynard & Horgan 2002a), but larvae of other species of *Acipenser* show consistent nocturnal activity (Kempinger 1988; Richmond & Kynard 1995).

Movement and Non-spawning Migrations

Generally Sturgeons migrate to optimize feeding and reproductive success. Downstream migrations are associated with feeding, especially for anadromous and semi-anadromous species; brackish and marine environments typically contain more food than freshwater habitats. Upstream migrations usually are associated with spawning (see reproductive section), although feeding may be involved (Auer 1996; Bemis & Kynard 1997). Migration also may be associated with avoidance of unfavorable environmental conditions (Auer 1996).

Potamodromous and amphidromous Sturgeons typically remain in their natal river basins or estuaries throughout their lives, but anadromous and semi-anadromus Sturgeons can range widely along the coast (Kynard 1997) with movements of ≤968 and 1,000 km (602 and 621 miles) for the Green Sturgeon and White Sturgeon, respectively (Erickson & Hightower 2007; Welch et al. 2006). For semi-anadromous species movement into saltwater habitats may occur shortly after spawning and adults may remain in salt water for all or most of the year, but some populations upstream of dams remain in fresh water all year. Abundance of forage and suitable thermal regimes likely dictate movement for most non-spawning individuals (Kynard 1997), and this may be true for potamodromous and anadromous species as well. All ripe adult Sturgeons demonstrate upstream migration in autumn, winter, and spring followed by downstream movement in summer and autumn (see the following subsection and reproduction section). Gulf Sturgeon males and females average 6.4 and 16.0 km/day (4.0 and 9.9 miles/day), respectively, as they move downstream from rivers into marine environments in autumn (Parkyn et al. 2007). Spawning migrations can cover almost 500 km (311 miles) for both *Acipenser* and *Scaphirhynchus* species with rates of ≤22 km/day (13.7 miles/day) (Wilson & McKinley 2004; Parkyn et al. 2007). But movement by non-spawning adults and early life history stages can be extensive and complex. Non-migratory movement is typically limited to <5 km/day (3.1 miles/day) and as little as <0.2 km/day (0.12 mile/day) for many species, but individuals can have extensive movements of >500 km (311 miles) (Bramblett & White 2001; Wilson & McKinley 2004; Hatin et al. 2007b; Parkyn et al. 2007). Gulf Sturgeons migrate along the coastline 15–302 km (9–188 miles) to specific areas of concentration that may represent overwintering grounds with abundant prey; areas are occupied by Gulf Sturgeons from different river systems and from genetically different populations (Edwards et al. 2007; Ross et al. 2009; Duncan et al. 2011; Parauka et al. 2011). Similar annual marine migrations are seen in the Green Sturgeon along the Pacific Continental Shelf with northern movement to Canadian overwintering grounds at 38 km/day (24 miles/day) and a return to U.S. waters in the spring at 40–58 km/day (25–36 miles/day) (Lindley et al. 2008). Home ranges of Sturgeons increase with age with yearling Lake Sturgeons averaging 2.5 km^2 (1 $mile^2$); age-2 Atlantic Sturgeons, 4 km^2 (1.5 $miles^2$); age-5 to age-13 Lake Sturgeons, 6 km^2 (2.3 $miles^2$); and adult Atlantic Sturgeons, 80 km^2 (30.9 $miles^2$) (Smith & King 2005b; Hatin et al. 2007b). Average home range of juvenile Pallid Sturgeons (15 km, 9.3 miles) was similar to that of adult Shovelnose Sturgeons (16.5 km, 10.3 miles) in the Missouri River (Gerrity et al. 2008).

Post-spawning migrations from freshwater to saltwater habitats may be complex for anadromous species. Sturgeons can reside in deep, freshwater holding areas during the summer along with non-spawned adults and subadults within the lower reaches of rivers. Feeding may or may not occur in fresh water. Autumn migration to a marine environment, where feeding occurs, coincides with short day length, falling water temperatures, and elevated river flow (Mason & Clugston 1993; Moser & Ross 1995; Erickson et al. 2002; Heise et al. 2005). Juveniles may migrate to brackish or marine environments with adults or may follow later (Auer 1996). Some Green Sturgeon post-spawning migrants move quickly into marine environments typically after peaks in discharge, but most move to discrete freshwater summer holding areas with low velocity and greater depth (5–10 m, 16.4–32.8 feet) for 44–199 days and then move downstream into marine environments in association with lower temperatures of 10–12°C (50–53.6°F) and significant increase in discharge (Benson et al. 2007; Erickson & Webb 2007). Post-spawning downstream migrations also occur in potamodromous species. Lake Sturgeons move quickly downstream after spawning, and this may help them avoid unfavorable temperatures and flows in spawning streams and increase foraging success in downstream or lake environments (McKinley et al. 1998; Auer 1999). Post-spawning migration in Shovelnose Sturgeons averages at least 41 km (25 miles) at 0.9 km/day (0.56 mile) (DeLonay et al. 2007).

Upstream migration by spawning adults must be complemented by downstream movement of early life history stages to either redistribute individuals throughout the range of the species (potamodromous species) or to transport young to appropriate rearing areas (anadromous and semi-anadromous species). This downstream migration begins with passive movement of Sturgeon larvae that is referred to as drift. Most Sturgeon larval drift data come from laboratory settings. Yolk-sac larvae of *Scaphirhynchus* and several Asian species of *Acipenser* and *Huso* are photopositive and begin to migrate downstream away from spawning grounds within the water column almost immediately after hatching and continue to migrate for 8–13 days. This rapid movement away from spawning areas may be to avoid predation or to move quickly to appropriate larval feeding habitat downstream. All species have light-colored bodies, and most have dark tails. Those with dark tails aggregate during downstream migrations; the movement of the dark tail may act as a visual signal to facilitate aggregation and group cohesion (Kynard et al. 2002ab, 2007; Zhuang et al. 2002, 2003). Yolk-sac larvae of the White Sturgeon also have light bodies, but are photonegative and have only a short, 2-day migration near the bottom (Kynard & Parker 2005). Yolk-sac larvae of the Green Sturgeon and Gulf Sturgeon have light bodies with dark tails; Gulf Sturgeon larvae do aggregate, but no downstream migration has been observed in these larvae (Kynard & Parker 2004; Kynard et al. 2005). The other North American *Acipenser* species (Shortnose Sturgeon, Atlantic Sturgeon, Lake Sturgeon) have yolk-sac larvae with dark bodies, and laboratory studies indicate they do not aggregate, are photonegative, and do not migrate at least initially (Kynard & Horgan 2002a; Kynard et al. 2003). Lake Sturgeon yolk-sac larvae are captured in drift nets below spawning grounds (Kempinger 1988; Smith & King 2005a; Benson et al. 2006). Yolk-sac larvae that do not show migration in a laboratory setting likely remain at the spawning site, suggesting the risk of predation at the spawning site is low (Richmond & Kynard 1995; Kynard & Horgan 2002a).

Most species of Sturgeons with migrating yolk-sac larvae continue to migrate as feeding larvae for 7–23 days, but feeding larvae of some Asian species and those of the White Sturgeon do not migrate (Kynard et al. 2002ab, 2007; Zhuang et al. 2002, 2003; Kynard & Parker 2005). Those species with larvae that only migrate while feeding can have short migration durations of 2–3 days (Shortnose Sturgeon), intermediate migrations lasting 12 days (Green Sturgeon), or long migrations of ≤45 days (Gulf Sturgeon) (Kynard & Horgan 2002a; Kynard & Parker 2004; Kynard et al. 2005). Most Sturgeon larvae drift only at night or have peak drift at night, but Shortnose Sturgeon and Pallid Sturgeon larvae migrate during daylight (Kynard & Horgan 2002a; Kynard et al. 2002a).

Longer migration times yield greater distances covered by drifting larvae, but this can vary due to current velocities, channel morphologies present at and downstream of spawning sites, and position of larvae in the water column. For example, Lake Sturgeon larvae typically drift for 11–26 km (6.8–16.2 miles) but can drift ≤61 km (37.9 miles) (Auer & Baker 2002; Smith & King 2005a; Benson et al. 2006). Vertical distribution of Lake Sturgeon larvae is neither benthic nor uniform but is concentrated in the upper 0.4 m (1.3 feet) of the water column (Caroffino et al. 2009). Data from drifting Shovelnose Sturgeon (1–10 days post-hatch) and Pallid Sturgeon (1–17 days post-hatch) larvae taken from a natural side channel of the upper Missouri River revealed that both species drift primarily within 0.5 m (1.6 feet) of the riverbed. Pallid Sturgeon larvae 5–13 days post-hatch released in the main stem of the upper Missouri River and sampled after drifting 5.7 km (3.5 miles) were nearly all captured within 0.5 m (1.6 feet) of the bottom, and most were concentrated in the high-velocity thalweg of the channel (Braaten et al. 2010). Shovelnose Sturgeon larvae averaged 0.090–0.16 m/s (0.30–0.52 foot/s) slower than the mean column water velocity compared with Pallid Sturgeon larvae that drifted at or just slightly slower (0.03–0.07 m/s, 0.10–0.23 foot/s) than mean column water velocity. Transition from drifting to a benthic life stage was initiated at 6 and 11–17 days post-hatch for Shovelnose Sturgeons (mean length 15.6 mm TL, 0.6 inch) and Pallid Sturgeons (18.1–20.3 mm TL, 0.7–0.8 inch), respectively, with much decreased drift rates of 0.20 m/s (0.66 foot/s) slower than mean water column velocity for 17-day post-hatch Pallid Sturgeon larvae. Drift simulations based on these data indicated that Shovelnose Sturgeon larvae drift for 94–250 km (58–155 miles) and Pallid Sturgeon larvae for 245–530 km (152–329 miles) (Braaten et al. 2008).

Downstream migration of early life stages of Sturgeons occurs in two general patterns as a parallel, but reverse pattern of that of the spawning migration of adults (see reproductive section). If a short, one-step migration is used by spawning adults, then a one-step migration by drifting larvae will allow them to reach rearing areas that would be just upstream of saline waters for anadromous species (e.g., Atlantic Sturgeon). If spawning adults undergo a long, one-step or two-step migration pattern, then early life stages use a two-step downstream migration, including an initial migration by larvae followed by a second migration by juveniles (e.g., Shortnose Sturgeon) (Kynard & Horgan 2002a). These migration patterns are only generalizations, as complex combinations of short or long downstream migrations of yolk-sac larvae, feeding larvae, or juveniles occur in different species and in different populations within a species (Kynard et al. 2002a; Kynard & Parker 2004, 2005; Kynard et al. 2005).

Resting

Summer resting areas for anadromous species (Green Sturgeon and Atlantic Sturgeon) are inhabited by recently spawned and non-spawned adults and subadults and are located in the lower reaches of rivers in fresh or low-salinity water. Individuals show little movement until migration to a marine environment occurs in autumn; Gulf Sturgeons do not feed while in these summer aggregation areas (Moser & Ross 1995; Sulak & Clugston 1999; Erickson et al. 2002; Hatin et al. 2002; Heise et al. 2005). Overwintering habitat for adult potamodromous Sturgeons includes deep (>6 m), slow water for the Lake Sturgeon (Rusak & Mosindy 1997) compared with shallow (1–2 m) channel crossovers with slow bottom flows for the Shovelnose Sturgeon (Quist et al. 1999). Semi-anadromous species overwinter in deep (10–27 m) saltwater estuaries and estuarine lakes (Wilson & McKinley 2004).

Chemosensory Systems and Feeding

Given the dorsolateral position of Sturgeons' eyes and the deep, turbid environment they typically inhabit, vision does not play a dominant role in feeding (Sillman et al. 1999; Miller 2004). Instead well-developed chemosensory systems are used. Olfaction allows for location of food items; external taste buds on the barbels and lips (extra-oral taste) trigger ingestion behavior, and internal oral taste buds determine whether food items are swallowed or rejected (Kasumyan 1999, 2002). In feeding larvae and juveniles of *Acipenser* and *Scaphirhynchus*, food odor stimulates feeding responses that include hovering close to the bottom with barbels trailing on the substrate as the fish moves in circular or S-shaped trajectories (scouring behavior). While swimming, the bodies of Sturgeons oscillate from side to side, allowing foraging over a wide area (Ross & Bennett 1997; Kasumyan 1999, 2002). Low concentrations of food odor (1 μM) elicit a feeding behavior response. The spectrum of amino acids that induce olfactory feeding responses in Sturgeons is narrow relative to that of other fishes and similar among species of Sturgeon. This contrasts with the taste system in Sturgeons that is highly species-specific, especially for oral taste. The extra-oral taste system is ≤10 times more sensitive relative to the oral system, is responsive to a broader spectrum of amino acids, and apparently develops more rapidly because it is the only well-developed taste system in larvae (Kasumyan 1999, 2002).

Additional Feeding-related Sensory Systems

Other sensory systems besides olfaction and taste likely also play a role in feeding. Vision may play an important role in helping *Acipenser* larvae detect and capture prey items as they alternate between foraging on the bottom and in the water column during downstream migration. The swift pursuit and capture of zooplankton in the water column likely is guided by the ability of Sturgeons to visually detect moving objects in illuminated habitat (Kynard & Horgan 2002a). Ampullary electroreceptors concentrated on the underside of the snout of Sturgeons also are likely used in feeding, and these structures are well developed in feeding larvae of *Acipenser* (Northcutt 1986; Miller 2004). Early larval foraging behavior in the Shovelnose Sturgeon and Atlantic Sturgeon occurs predominantly in the water column with foraging at the water-air interface, including swimming inverted with the ventral surface up. As these larvae develop they switch to mostly benthic feeding. Larvae of the Lake Sturgeon use benthic feeding throughout their development (Ross & Bennett 1997; Kynard & Parker 2004).

Camouflage Coloration

Larvae of some species of *Acipenser* and all species of *Scaphirhynchus* studied to date (Pallid Sturgeon and Shovelnose Sturgeon) have light bodies and black tails that may provide cryptic coloration in benthic and drifting (mid- to upper-water column) habitats, and the wig-wag swimming motion of the black tail in feeding larvae may create a confusing strike zone for predators (Kynard et al. 2002b; Gisbert & Ruban 2003; Kynard & Parker 2005). Young Shortnose Sturgeons and Lake Sturgeons have black blotches that break up the body pattern and may act as camouflage; the blotched pattern disappears in subadults. Even so, bony plates and sharp scutes may provide all the protection from predation necessary for juvenile Sturgeons; hence, the advantage of blotched coloration is uncertain (Scott & Crossman 1973; Wallus 1990a).

Jumping and Sound Production

Species of *Acipenser* frequently jump entirely out of the water. Jumping may occur to produce sounds used in communication in the Gulf Sturgeon (Sulak et al. 2002), but jumping observed in the Lake Sturgeon and Atlantic Sturgeon may serve to remove attached parasitic lampreys (Becker 1983; Scott & Scott 1988). Jumping also occurs in the Lake Sturgeon before and during spawning activities adjacent to spawning sites in association with a more common porpoising behavior (see reproduction section), but the purpose is unknown (Bruch & Binkowski 2002).

Distinct aural signals are produced by Sturgeons (see also reproduction section). Gulf Sturgeons, as well as other Sturgeons, frequently jump out of the water, and the sound produced may be a form of communication to maintain group cohesion. Jumping is prevalent during the summer when Gulf Sturgeons congregate in deep holding areas in rivers; feeding does not occur during this time. The greatest number of jumps occurs in June with peak activity in all summer months near dawn and to a lesser degree near sunset. Sonograms revealed nine distinct sounds, including acoustic signatures produced by exit, reentry, and splash subsidence that differed from the sounds of jumping Striped Mullet (*Mugil cephalus*) and of dropped objects. Because of the significant energy cost of jumping during a fasting period, this behavior likely provides some benefit to the Gulf Sturgeon. This, coupled with the distinctive sounds produced, suggests that jumping is a form of communication (Sulak et al. 2002). Jumping also occurs in estuary and marine habitats for Gulf and Green Sturgeons (Edwards et al. 2007; Erickson & Hightower 2007).

REPRODUCTION

Seasonality

Worldwide Sturgeons spawn in all seasons and in variable water flow and temperature conditions (Bemis & Kynard 1997). All North American Sturgeons typically spawn in the spring with some southern populations spawning as early as February and Sturgeons in northern areas extending spawning into late June (Tables 5.1 and 5.2; Wilson & McKinley 2004; Beamesderfer et al. 2007). Populations of the Atlantic Sturgeon in southern South Carolina can make two spawning runs. Some migrate upriver from the Atlantic to spawn in autumn with males and females running ripe and spent females found later in the season; histological examination of gonad biopsies verified spawning. The two season spawning events are corroborated with strong bimodal length distribution of age-1 Atlantic Sturgeons in the Edisto River, South Carolina. Autumn migrants are typically smaller than those making spring spawning runs (Smith et al. 1984; Collins et al. 2000a; McCord et al. 2007). Small numbers of gravid and running Gulf Sturgeon females and males are captured in autumn in the Suwannee River, Florida, with late spring capture of small juveniles equivalent in size to 6- to 10-month-old fish (Sulak & Clugston 1998). Capture of Shovelnose Sturgeon milting males, females with ripe eggs, males and females with elevated plasma sex steroid concentrations, and larvae in the Mississippi River in autumn indicate an autumn spawn, but the contribution of autumn cohorts to the population is unknown (Divers et al. 2009; Stahl et al. 2009; Tripp et al. 2009b).

Age at Sexual Maturity

Sturgeons have late sexual maturation (Tables 5.1 and 5.2) that is an important life history parameter to consider in their conservation and management (Birstein 1993; Bemis & Kynard 1997). Aging techniques, however, may underestimate the actual age at sexual maturity (see ecology section). Size actually may be more important than age in the initiation of maturation (Caron et al. 2002). Males mature sooner than females, but a wide range of maturation ages is present between and within species, particularly across sizes and latitudes. Small, more southern species or populations mature sooner than large, more northern species or populations (Dadswell 1979; Smith 1985; Billard & Lecointre 2001; Auer 1999). The Shovelnose Sturgeon is a smaller relative of the Pallid Sturgeon, and female Shovelnose Sturgeons mature at 6–12 years versus 15–20 years in the larger species; males of both species mature at ≥5 years old (Keenlyne & Jenkins 1993; Keenlyne 1997; Kennedy et al. 2006; Tripp et al. 2009b; Stahl et al. 2009). Shortnose Sturgeons, the smallest North American species of *Acipenser*, mature at 2–5 years (males) and 4–5 years (females) in southern populations, but northern populations mature at 11–12 years (males) and 12–18 years (females) (Dadswell 1979; Kynard 1997). This contrasts with the intermediate-sized Green Sturgeon, which matures at 14–16 years (males) and 16–20 years (females) (Van Eenennaam et al. 2006), and the larger Lake Sturgeon in which northern populations mature at older ages of 15–20 years (males) and 22–33 years (females) (McLeod et al. 1999). The largest species of *Acipenser* have a wide range of maturation ages, from 5 to 34 years for the Atlantic Sturgeon to 11 to 34 years for the White Sturgeon (Cochnauer et al. 1985; Smith 1985). Many Sturgeons mature earlier in captivity due to warmer water temperatures and high-quality commercial feed. Late-maturing, wild White Sturgeons typically attain early maturity in captivity at 3–4 years for males and 6–14 years for females (Birstein 1993; Doroshov et al. 1997; Van Eenennaam et al. 2004).

Natal Fidelity

Several species of *Acipenser* show high levels of fidelity to the rivers in which they were spawned, migrating in winter or spring into those rivers to spawn themselves. Genetic studies demonstrated natal fidelity in the Shortnose Sturgeon, Atlantic Sturgeon, and Gulf Sturgeon (e.g., King et al. 2001; Grunwald et al. 2002; Dugo et al. 2004). Likewise, molecular and tagging studies demonstrated fidelity to rivers and sites within rivers in adult Lake Sturgeons (Lyons & Kempinger 1992; Auer 1999; Knights et al. 2002; DeHaan et al. 2006). Site fidelity can arise from either particular characteristics of the site or from homing through olfactory imprinting in larvae as they begin to feed, but the specific means used by Sturgeons to return to their natal rivers is unknown and needs to be tested (Boiko et al. 1993; Bemis & Kynard 1997; Kasumyan 1999).

Spawning Migrations

The distance covered during spawning migrations by *Huso* and *Acipenser* species is correlated positively with average adult size. The smallest North American species of *Acipenser*, the Shortnose Sturgeon, typically migrates ≤200 km (124 miles) compared with the largest species, the White Sturgeon, which can migrate ≤1,200 km (746 miles). Similarly, some large Asian Sturgeons have spawning migrations of 3,300 km (2,051 miles). But not all North American species follow this trend. Lake Sturgeons are mid-sized with short migrations of usually <100 km (62 miles) (Auer 1996). Upstream migration for the Shovelnose Sturgeon in the lower Missouri River averages ≥175 km (109 miles) at 5.6 km/day (3.48 miles) with an upper range of 388 km (241 miles) and 12.75 km/day (7.92 miles) (DeLonay et al. 2007).

Spawning Migration Patterns

Three basic patterns occur in Sturgeon spawning migrations. One-step spawning migrations entail a direct upstream migration to the spawning site in the winter or spring followed immediately by spawning, then a return downstream. Spawning usually occurs in the middle or lower reaches of rivers. This is the most common pattern of spawning migration in Sturgeons. The short, two-step spawning migration involves an upstream movement in autumn, overwintering near the spawning area, then a short migration in the spring to the spawning site. Middle and upper reaches of rivers are usual spawning locations for these migrants. Long, two-step spawning migrations are those in which Sturgeons make an initial upstream migration to an oversummering or overwintering area (or both) and then make a long upstream migration to the spawning site. Only large Sturgeons, including the White Sturgeon in the Columbia River, have the long, two-step spawning migration pattern (Bemis & Kynard 1997).

Patterns of spawning migrations can vary within species and even within a population or individual. Spawning migrations of the Shortnose Sturgeon can occur in one of three patterns: a short, one-step migration in the spring initiated only a few weeks before spawning; a long, one-step migration lasting many weeks during late winter and spring; and a two-step migration consisting of a long autumn migration to an overwintering area near the spawning site followed by a short spring migration. The short, one-step migration occurs when spawning grounds are near estuaries; pre-spawning adults cease foraging about 5 months before spawning. The long, one-step and two-step migration patterns occur when spawning grounds are ≥60 km (37 miles) from estuaries with the two-step typically more prevalent for longer migrations (≥140 km, 87 miles). Spawning grounds may have both long, one-step and two-step migrants present, where they appear to spawn together. In southern rivers, long, one-step migrations >200 km (124 miles) occur that may reflect greater energy resources due to warmer water and perhaps winter feeding (Kynard 1997). In contrast to the anadromous Shortnose Sturgeon, the potamodromous Lake Sturgeon has a relatively simple and consistent autumn pre-spawning migration from lake or downstream habitats to deep holes within tributary river systems. These winter staging areas are often adjacent to spawning sites (Kempinger 1988; McKinley et al. 1998; Bruch & Binkowski 2002).

Spawning Territories

Sturgeons do not exhibit any territoriality, but male Lake Sturgeons maintain position at a spawning site for the duration of spawning activities (2 weeks), and they will continue to stage near spawning grounds for ≤1 month if gravid females are present awaiting warmer water temperatures to spawn a second time (Bruch & Binkowski 2002).

Spawning Frequency

Sturgeons typically do not spawn every year in the wild, and most have multiple years between spawning events. The reproductive hiatus is typically longer for females, northern populations within a species, and larger species. Male and female Shovelnose Sturgeons and male Pallid Sturgeons spawn at 2- to 3-year intervals, but female Pallid Sturgeons range from 3 to 10 years between spawning events (Mayden & Kuhajda 1997b; Kennedy et al. 2006; Tripp et al. 2009b). Large species of *Acipenser* have extensive ranges for spawning intervals, including 3–11 years for both sexes in White Sturgeons and 2–7 years for male and 3–12 years for female Lake Sturgeons (Cochnauer et al. 1985; Auer 1999; Peterson et al. 2003). The smaller Shortnose Sturgeon has relatively short spawning intervals of 2 years for males and 3–5 years for females in northern populations compared with every year for males and perhaps every 1–2 years for females in more southern populations (Dadswell 1979; Kieffer & Kynard 1993; Kynard 1997). Green Sturgeons also have a relatively short spawning frequency of 2–4 years (Beamesderfer et al. 2007; Erickson & Webb 2007). The Atlantic Sturgeon is one of the largest North American species, but males spawn every year and females every 3 years with both sexes having intervals ≤5 years (Smith 1985; Collins et al. 2000a; Fox et al. 2000). With less variable temperatures and more food availability in captivity, some species show a shortened time between spawning events relative to wild populations. In captive Siberian Sturgeon populations (*Acipenser baerii*), e.g., males spawn every year and females spawn every 1.5–2 years (Birstein 1993).

Spawning Modes and Location

Sturgeons typically are considered broadcast spawners, releasing large numbers of eggs over extensive areas of river bottom (Tables 5.1 and 5.2; Cherr & Clark 1985; Parsley et al. 1993, 2002), more specifically referred to as lithophilic riverine spawners (explicitly the genus *Acipenser*), meaning spawning in close proximity or directly on hard or rocky substrates (Fig. 5.12; Sulak & Clugston 1999; Bruch & Binkowski 2002).

Upstream spawning migrations occur in all species with potamodromous Sturgeons entering tributaries to lakes or large rivers or using borders of main channels. Semianadromous and anadromous species leave marine, brackish, or estuarine habitats to spawn in the river main stem. Spawning occurs at temperatures from 17 to 21°C (63–70°F) in *Scaphirhynchus* and 8.8 to 21.5°C (47.8–70.7°F) for most *Acipenser*; Gulf Sturgeons spawn in slightly warmer waters (18.3–23°C, 64.9–73.4°F) (Bruch & Binkowski 2002; Wilson & McKinley 2004; Beamesderfer et al. 2007; Erickson & Webb 2007). All North American Sturgeons require strong flows over hard substrates at spawning sites, often in the swiftest water available. Spawning substrates are typically hard bottoms consisting of hard clay, gravel, rubble, boulders, bedrock, and rocky ledges in high-velocity areas ≤2.4 m/s (7.9 feet/s) near the substrate (Fig. 5.12; Parsley et al. 1993; Wilson & McKinley 2004). Some spawning sites for Lake Sturgeons have flow of <0.5 m/s (1.6 feet/s) (Manny & Kennedy 2002), and the average flow at spawning sites of the Shortnose Sturgeon is only 0.7 m/s (2.3 feet/s) (Kynard 1997). Spawning occurs at depths of 0.5–27 m (1.6–89 feet) (Parsley et al. 1993; Fox et al. 2000; Bruch & Binkowski 2002; Wilson & McKinley 2004). Channel habitat is used by the Shortnose Sturgeon, where depth may be less important than bottom water velocity, which ranges from 0.4 to 1.8 m/s (1.3–5.9 feet/s); high discharge can negatively affect spawning success (Kynard 1997). In an unregulated river, White Sturgeons used side channels as spawning sites, all life stages were captured at depths less than those reported for regulated rivers, and a wider array of habitats was used, this all likely due to the higher turbidity levels relative to regulated rivers (Perrin et al. 2003).

Spawning of Gulf Sturgeons in the Suwannee River, Florida, only occurs in a section where water chemistry includes slightly alkaline pH and calcium concentrations of 6–18 mg/l, even though suitable substrate and flow are available in adjacent upstream and downstream segments of the river (Sulak & Clugston 1999). Water at a spawning site must have calcium or magnesium ions present in sufficient concentration for the adhesive jelly that surrounds an egg to be activated if fertilization or development is to occur, but if calcium ion or pH levels are too high then sperm may have premature acrosome reactions, and egg fertilization will not be realized (Cherr & Clark 1985).

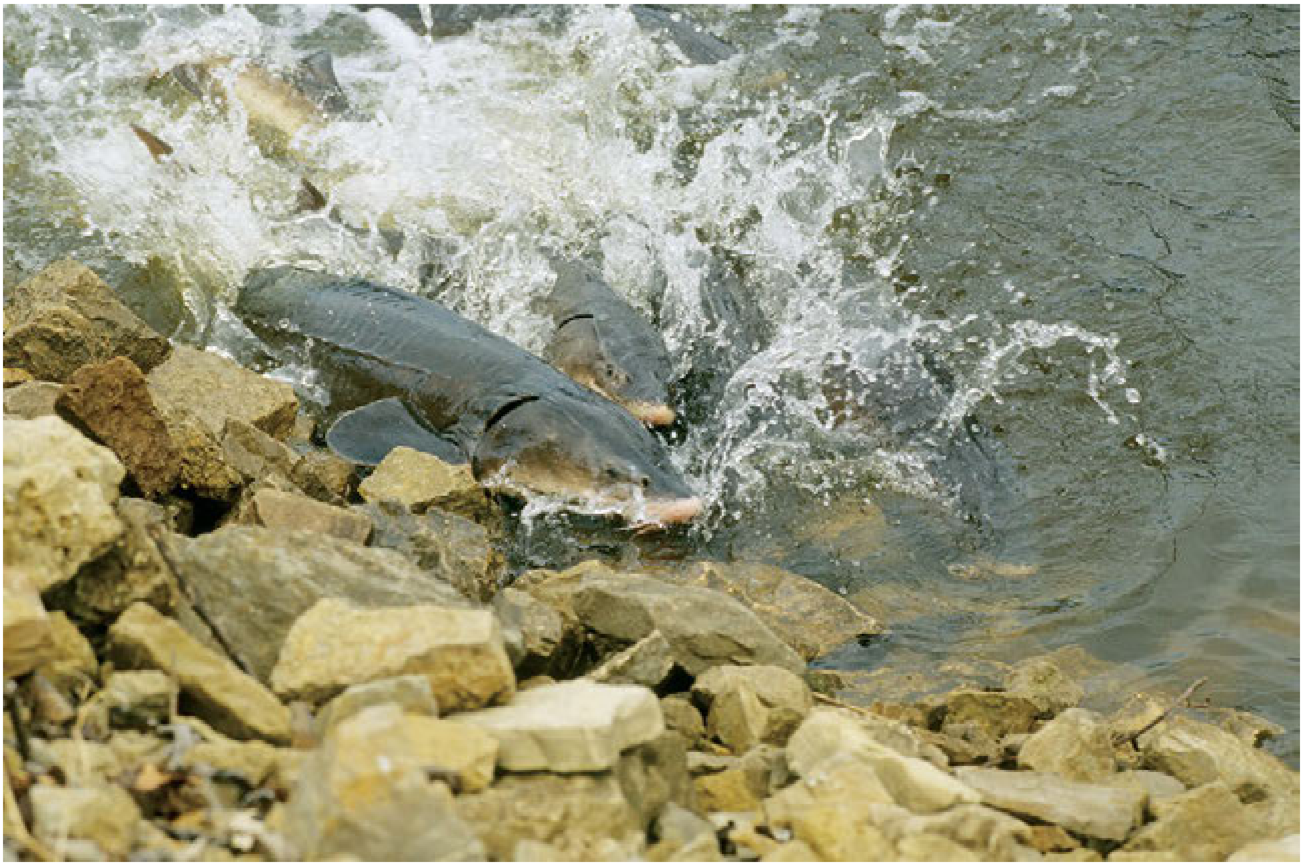

Figure 5.12. Lake Sturgeons, *Acipenser fulvescens*, spawning over rocks in the Wolf River, New London, Wisconsin, April 2010 (photograph by and used with permission of ©Engbretson Underwater Photography).

Courtship

Sturgeons do not exhibit any typical courtship behavior, but a porpoising behavior observed in the Lake Sturgeon may have some courtship purpose. During this behavior Lake Sturgeons stick their heads out of the water as they swim upstream, occasionally jumping entirely out of the water. Once submerged the Lake Sturgeon expels air and produces a trail of bubbles. This behavior occurs in the main channel adjacent to the spawning site and begins ≥14 days before spawning at water temperatures of 6.6–16.0°C (43.9–60.8°F); it continues through peak spawning (Bruch & Binkowski 2002).

Sound Production during Spawning

Sturgeons produce sound while spawning (see also behavior section). Lake Sturgeon males produce a rapid succession (4–5 beats/s) of dull thuds or wumps that coincides with the beats of their tails against the abdomens of females during the spawning act and can be felt as a vibration on the river bank. The sound appears to be produced internally and not from males hitting females with their tails; the thud sounds are also made by males making spawning runs without females. When the noise is produced, other males 3–5 m (9.8–16.4 feet) downstream of the spawning site swim quickly to the area, but females do not react (Bruch & Binkowski 2002). Russian species of *Acipenser* and *Huso* also produce sound, and Sturgeons do respond to recorded sounds, but the role these sounds play in behavior is unknown (Johnston & Phillips 2003). The Pallid Sturgeon and Shovelnose Sturgeon produce four distinct sound types with different duration, frequency, and harmonics. These include low-frequency (90–420 Hz) knocks and moans, which may travel long distances, and high-frequency (510–4,200 Hz) squeaks and chirps (Johnston & Phillips 2003). The low-frequency knocks and moans are within the optimum range of audible frequencies and may serve as some form of communication, but squeaks and chirps are mostly well outside of this range and are likely incidental and not useful for communication (Lovell et al. 2005). The mechanism for sound production in Sturgeons is unknown, but similar sounds in other fishes are produced by contracting muscles associated with the gas bladder (Bruch & Binkowski 2002; Johnston & Phillips 2003). As noted (see morphology section), Sturgeons have hair cells aligned in both horizontal and vertical planes within the inner ear that provide evidence for directional hearing (Lovell et al. 2005).

Spawning

Most of the detailed information on Sturgeon spawning is from species of *Acipenser* in which water temperature or water temperature and lunar cycles trigger spawning. In Lake Sturgeons in tributaries of Lake Winnebago, Wisconsin, temperature is the key environmental signal affecting the timing and length of the spawning period. Males and females migrate from winter staging areas into rivers shortly after ice disappears and concentrate in 2–10 m (6.6–32.8 feet) deep pools adjacent to or ≤3 km (1.9 miles) from spawning sites. At temperatures of 8.3–16°C (46.9–60.8°F) males move onto spawning sites 1–2 days before females and begin cruising along the entire site, searching for ovulating females. Spawning begins when ovulating females move onto the site. Active spawning occurs over a wide temperature range (8.3–21.1°C, 46.9–70°F) with the peak occurring at 8.3–16.0°C (46.9–60.8°F). A decrease in water temperature of 1–7°C (2–13°F) can interrupt spawning for 2–25 days, and temperatures must typically climb 1–2°C (2–4°F) above the initial spawning conditions for spawning to resume (Kempinger 1988; Bruch & Binkowski 2002). Spawning occurs during the day and night and typically lasts 1–4 days on a site (Fig. 5.12). Spawning ends for the season at temperatures from 15.0 to 21.1°C (59.0–70.0°F) with males and females rapidly dispersing downstream (Bruch & Binkowski 2002).

Sex pheromones may allow for mature male Sturgeons to detect ripe females by olfaction at spawning sites. Prespawning mature male Shortnose Sturgeons can detect the odor from conspecific females in a laboratory setting (Kynard & Horgan 2002b). Post-ovulatory ovarian fluids of Asian *Acipenser* caused increased swimming speed in mature males held in tanks with some individuals demonstrating brief convulsive body movement (Kasumyan 1999).

Temperature and the lunar cycle are key environmental factors affecting the timing of spawning in the Gulf Sturgeon. Pre-migratory individuals stage in river mouths and estuaries in mid- to late February, perhaps as a physiological necessity to move from salt water to fresh water. Rivers must reach 17°C (62.6°F) for spawning migration to commence, but the first major upstream run of prespawning females does not commence until just after the new moon in March, followed by spawning 4–7 days later. Spawning occurs for ≤23 days, ceasing when water temperatures rise to 21–22°C (69.8–71.6°F). Spawning was interrupted for 14 days even though temperatures remained cool; the hiatus was centered on a full moon. Based on development of fertilized eggs collected at daybreak, spawning occurs at night (Sulak & Clugston 1999).

Fewer details are available on spawning for species of *Scaphirhynchus*, but spawning readiness based on the presence of reproductively ready Shovelnose Sturgeon females in the lower Missouri River appears to be associated with photoperiod followed by temperature with another set of short-term cues signaling ovulation and spawning (Papoulias et al. 2011). Data from the Mississippi River indicate that peak Shovelnose Sturgeon spawning likely coincides with rising river stages and temperatures between 16.9 and 20.5°C (62.4–68.9°F). Under these river conditions females with ripe eggs and milting males are most abundant, followed by peak capture of spent Shovelnose Sturgeons and greatest abundance of age-0 individuals (Tripp et al. 2009b; Phelps et al. 2010b).

In Lake Winnebago, Wisconsin, Lake Sturgeons spawn at sites with clear water at depths of ≤1 m, so that detailed spawning observations are possible (Bruch & Binkowski 2002). A female moves onto the spawning site and is at first inactive and ignored by males. After about 1 h, the female begins to ovulate and is ready to lay eggs. She is joined typically by a single male, which moves on either side of her from behind, nosing her on the side and abdomen. As the female begins to move upstream the male quickly pounds the female's abdomen with his tail as he moves forward and releases sperm. Almost immediately 1–5 other males join the first male, pounding the female's abdomen with their tails and releasing sperm. Estimates of 947–1,444 eggs and 200–800 billion sperm are released / spawning bout. During the spawning bout, which lasts 2–4 s, males produce a dull thudding noise (see behavior section). Females slowly drift back downstream and then begin another spawning bout with 33–240 s between bouts. Over 8–12 h of repeating this sequence, a female spawns until all of her mature eggs are discharged. Males lie against a rock or log between bouts, but soon begin cruising for spawning females (Bruch & Binkowski 2002). In the St. Lawrence River, Quebec, Atlantic Sturgeon males move back and forth between spawning areas, likely a searching behavior for females (Hatin et al. 2002; see also Fox et al. 2000).

Parental Care

Sturgeons do not exhibit any parental care. In fact, breeding male Lake Sturgeons were observed eating Lake Sturgeon eggs on the spawning site (Kempinger 1988; Bruch & Binkowski 2002).

Breeding Systems

In the Lake Sturgeon, and potentially all Sturgeons, the breeding system is polygamous (both sexes breeding with >1 individual). This includes polyandry with each female spawning with numerous males both within a single spawning bout and over the 8- to 12-h spawning period, and polygyny, in which males remain at the spawning site for the duration of spawning activity (1–4 days) and spawn with numerous females. This polygamous breeding system maximizes the genetic diversity of offspring (Bruch & Binkowski 2002). In contrast, Shortnose Sturgeons might form pair bonds as suggested by the capture of the same individuals side by side after 1- to 3-year intervals (Dadswell 1979).

Sex ratios in Sturgeons can vary between and within species, but general patterns are evident when comparing the general population versus populations at spawning sites and comparing different size classes. When populations are sampled in all or several seasons or data are gathered from sport or commercial harvest, sex ratios are typically nearly equal for the Lake Sturgeon, White Sturgeon, Green Sturgeon, and some populations of the Atlantic Sturgeon and Shovelnose Sturgeon (Threader & Brousseau 1986; DeVore et al. 1995; Van Eenennaam & Doroshov 1998; Auer 1999; Colombo et al. 2007c; Webb & Erickson 2007) but favor females in ratios ≥2.8F:1M for the Shortnose Sturgeon and Pallid Sturgeon, and some populations of the Atlantic Sturgeon and Shovelnose Sturgeon (Dadswell 1979; Smith et al. 1984; Carlson et al. 1985). Higher numbers of females likely are the result of their longer lifespan, a supposition supported by dominance of females in larger size classes (Probst & Cooper 1955; Dadswell 1979; Beamesderfer et al. 1995). In contrast, males outnumber females during spawning runs and at spawning sites for all species of Sturgeons examined with ratios ≥9.6M:1F (Lyons & Kempinger 1992; Carr et al 1996; Van Eenennaam et al. 1996, 2006; Auer 1999; Collins et al. 2000a; Kennedy et al. 2006). The skewed sex ratio in spawning populations of Sturgeons (effective sex ratio) is in favor of males because of the shorter interval between spawning events for males and the greater amount of time they spend at the spawning site (Auer 1999; Van Eenennaam et al. 2006). The sex ratio is even more skewed when considering that males mature much earlier than females (operational sex ratio) (Bruch & Binkowski 2002).

Fecundity

Sturgeons are large fishes that release large numbers of eggs over extensive areas of river bottom (Tables 5.1 and 5.2; Cherr & Clark 1985; Parsley et al. 1993, 2002), e.g., ≤2.6 million eggs in the Atlantic Sturgeon (Van Eenennaam & Doroshov 1998). But most Sturgeon species have substantially lower fecundity compared with other fishes with similar spawning modes; that fact, along with their late maturation, are among the main factors that make Sturgeons susceptible to overfishing (Boreman 1997). As with most fishes, egg production increases with female Sturgeon size, both among and within species, and more fecund species have smaller mature (stage-5) eggs. The two largest North American Sturgeons, Atlantic and White Sturgeons, produce ≤2.6 and 1.5 million mature eggs/female (absolute fecundity) for a 231 cm FL (91 inch) and a 309 cm TL (122 inch) female, respectively, but smaller females (183 and 135 cm FL or 72 and 53 inches) have absolute fecundities of 400,000 and only 98,200 eggs. Relative fecundity (number of eggs/kg or pound of body weight) range from 7,000 to 22,000 eggs/kg (3,175–9,980/pound) for Atlantic Sturgeons. Mature egg diameter is 2.38–2.93 mm (0.09–0.12 inch) for Atlantic Sturgeons and 3.5–4.0 mm (0.14–0.16 inch) for White Sturgeons (Cherr & Clark 1985; Dettlaff et al. 1993; DeVore et al. 1995; Van Eenennaam et al. 1996; Boreman 1997; Van Eenennaam & Doroshov 1998). The Lake Sturgeon, a mid-sized *Acipenser* species, averages 383,529–425,000 eggs/female and has an average relative fecundity of about 11,000 eggs/kg (5,000/pound) at a female weight of 21.3–42 kg (47–93 pounds). Mature egg diameters are 2.6–3.5 mm (0.10–0.14 inch) (Scott & Crossman 1973; Bruch & Binkowski 2002; Bruch et al. 2006). Absolute fecundity for the smaller Shortnose Sturgeon ranges from only 27,000 to 208,000 eggs, but has a similar average relative fecundity of 11,568 eggs/kg (5,247/pound) at a female weight of 3–19 kg (7–42 pounds). Mean egg diameter is 3.1 mm (0.12 inch) (Dadswell 1979). Although intermediately sized, the Green Sturgeon is relatively less fecund than other species, producing only 52,000–242,000 eggs/female or a relative fecundity of 1,900–4,200 eggs/kg (862–1,905/pound) at a female size of 153–203 cm FL (60–80 inches). But they have the largest egg diameter of any North American Sturgeon at 4.04–4.66 mm (0.16–0.18 inch) (Van Eenennaam et al. 2001, 2006). Within *Scaphirhynchus*, a large female Pallid Sturgeon (41 years old and 140 cm FL, 55 inches) produced 170,000 eggs or a relative fecundity of 9,936 eggs/kg (4,506/pound). Mean egg diameter was 2.0–2.5 mm (0.08–0.10 inch) (Keenlyne et al. 1992). Smaller Shovelnose Sturgeons have a similar average egg diameter (2.6 mm, 0.10 inch), but lower absolute fecundity and higher relative fecundity. Fecundity can vary between Shovelnose Sturgeon populations with 7,069–16,708 eggs/female in the Missouri River compared with 13,241–65,490 eggs/female in the Wabash River, Indiana (62–86 cm FL or 24–34 inches for Wabash River), but relative fecundity can be similar with 13,090–25,080 eggs/kg (5,938–11,376/pound) in the Missouri River and 11,220–23,956 eggs/kg (5,088–10,866/pound) in the Wabash River (Kennedy et al. 2006; Bryan et al. 2007). In the middle Mississippi River absolute and relative fecundity varies greatly between individuals, from 5,733–81,842 eggs/female (55.9–76.7 cm FL or 22.0–30.2 inches) and 6,220–46,230 eggs/kg (2,821–20,970/pound) (Tripp et al. 2009b).

Gametes

Sturgeons (and the Paddlefish) are unique in that sperm possess an acrosome even though eggs have a micropyle, and Sturgeon eggs are unique in having numerous micropyles (3–15). An acrosome is a cap over the sperm head that contains enzymes involved in sperm penetration through the extracellular envelope (chorion) of the egg. Most Ray-finned Fishes (Actinopterygii) have eggs with a single funnel-shaped micropyle at the animal pole that allows a single sperm to make direct contact with the inner plasma membrane of the egg for fertilization, eliminating the necessity for an acrosome on sperm. Sturgeon sperm, however, retain an acrosome even though their eggs have numerous micropyles. Within vertebrates, only Lampreys (Petromyzontidae), Hagfishes (Myxinidae), Sturgeons, and the Paddlefish possess an acrosomal process. When the Sturgeon's acrosome is activated, a fertilization filament (acrosomal process) forms that aids in fertilization, but the exact function of the filament is unknown. Numerous micropyles and other gamete morphologies and functions are potential reproductive adaptations for Sturgeons to successfully broadcast-spawn in a riverine environment (see physiology section; Cherr & Clark 1985; Psenicka et al. 2011).

Embryo Characteristics and Development

Fertilized eggs (embryos) are adhesive and therefore attach to the surface of hard substrates; they are found in interstitial spaces 10–20 cm (4–8 inches) below the substrate surface (Bruch & Binkowski 2002). The timing of development is dependent on incubation temperatures with faster development at higher temperatures (4.6–5.8 days at 16–20°C, 60.8–68°F) for the Atlantic Sturgeon, Shortnose Sturgeon, and Shovelnose Sturgeon and only 2.3–2.5 days at 22.2–23.3°C (72–73.9°F) for Gulf Sturgeons (Smith et al. 1980; Parauka et. al 1991; Kynard 1997; Colombo et al. 2007b). Typically, however, Sturgeon embryos hatch in 7–13 days at 12–16.5°C (53.6–61.7°F) (Richmond & Kynard 1995; Kynard 1997; Deng et al. 2002; Snyder 2002). Viable temperatures for embryonic development range from 8.3°C (46.9°F) for northern Lake Sturgeon populations to ≤20°C (68°F) for Gulf Sturgeons (Bolker 2004).

Thirty-six developmental stages, from the unfertilized egg through hatching, are identified for Sturgeons (Dettlaff et al. 1993; Colombo et al. 2007b) (Table 5.3). Major stages include fertilization, cleavage, blastula formation, gastrulation, neurulation, and organogenesis. Sturgeons undergo holoblastic cleavage in which each cleavage divides the entire egg cytoplasm, including the yolk. Because Sturgeon eggs are large and have significant amounts of yolk concentrated at the vegetal pole, the process of cleavage is slow except at the animal pole, so that when the first cleavage is complete at the vegetal pole several more already have formed at the animal pole (Bolker 2004; Colombo et al. 2007b). Sturgeon embryos have hatching glands (at the ventral base of the head in the Shovelnose Sturgeon) that secrete a hatching enzyme that makes the chorion soft and then fragile to assist embryos in hatching (Deng et al. 2002; Colombo et al. 2007b).

The size of Sturgeons at hatching is related to the size of the egg and its yolk. Hatchlings of the Atlantic Sturgeon and Gulf Sturgeon are the smallest of all North American *Acipenser*, with larvae averaging 7.1 and 8.3 mm TL (0.28 and 0.33 inch) and having the smallest mature eggs (average 2.62 and 2.21 mm, 0.10 and 0.09 inch diameter) (Smith et al. 1980; Parauka et al. 1991; Bardi et al. 1998;

Table 5.3. Stages of embryonic development of Shovelnose Sturgeons, *Scaphirhynchus platorynchus*, reared at 20°C (68°F) (Colombo et al. 2007b).

Stage	Time Post-Fertilization	Description of Embryo
1	0 h	Fertilization, formation of light spot at apex of animal pole
2	0.75 h	Disappearance of polar spot after 1 mitotic interval
3	1 h	Formation of eccentric crescent band in animal pole
4	2 h	Formation of first cleavage furrow after 2.5 mitotic intervals
5	3 h	Formation of second cleavage furrow after 4 mitotic intervals
6	4 h	Formation of third cleavage furrows after 5 mitotic intervals, furrow into vegetal pole
7	5 h	Formation of fourth cleavage furrow after 6.5 mitotic intervals, full cleavage in vegetal pole
8	6 h	Formation of fifth cleavage
9	7 h	Continued division in vegetal pole
10	8 h	Formation of cleavage cavity in animal pole
11	9 h	Early blastula, small blastomeres still visible in animal pole
12	11 h	Late blastula, animal pole surface smooth
13	17 h	Onset of gastrulation, band between animal and vegetal poles
14	18 h	Formation of dorsal blastopore lip, blastocoel seen through thin cell layer at animal pole
15	23 h	Two-thirds of embryo covered by blastoderm, primitive gut present
16	25 h	Large yolk plug evident, blastocoel ring-like on ventral surface
17	27 h	Small yolk plug, blastocoel dark spot on ventral surface, blastoderm covering most of embryo
18	29 h	Gastrulation complete, formation of slit-like blastopore
19	29 h	Onset of neurulation, neural plate and neural groove present
20	31 h	Neural groove wider, neural fold appears in head region
21	35 h	Excretory rudiments evident, neural folds thicken
22	35 h	Excretory rudiments elongate, neural folds close anteriorly, neural tube begins to close in caudal region
23	36 h	Neural tube closed, different brain regions begin to form
24	39 h	Excretory rudiments thicken anteriorly, eye vesicles form, first pair of visceral arches appear
25	45 h	Eye rudiments clearly visible, second pair of visceral arches appear, lateral plates evident to anterior of head, tail thickens, pronephros present as tubes, first somites appear
26	52 h	Heart rudiment forming with fusion of lateral plates and prosencephalon, tail rudiment separating from yolk sac, third pair of visceral arches appears
27	54 h	Heart rudiment as short tube, eye rudiments as slits, head thickens and separates from yolk sac, somites covering body
28	60 h	Heart rudiment elongates, tail continues to elongate, fin fold appears
29	63 h	Onset of heartbeat, heart S-shaped, embryo bent, hatching glands pronounced, olfactory sacs present
30	81 h	Tail begins to straighten, fin folds evident, eye cups evident, hatching glands thickened
31	85 h	Tail approaches heart, head deep and most cranial part separated from yolk-sac membrane, pronephros difficult to distinguish
32	87 h	Tail end reaches head, fin fold formed, head continues to separate from yolk sac
33	*	Tail straightens fully if embryo removed
34	*	Embryo capable of movement
35	93 h	Hatching of advanced embryos, embryo clear with no pigment in eye cups, yolk sac yellow, pigment plug not fully formed
36	102 h	Mass hatching; well-developed yolk plug, proto-larvae swim up in water column

* Stage not seen.

Van Eenennaam & Doroshov 1998). Newly hatched larvae of the White Sturgeon and Green Sturgeon are the largest at 10–11 and 12.6–15 TL mm (0.39–0.43 and 0.50–0.59 inch) and have the largest mature eggs (3.5–4.0 and 4.04–4.66 mm, 0.14–0.16 and 0.16–0.18 inch diameter), respectively (Cherr & Clark 1985; Van Eenennaam et al. 2001, 2006; Deng et al. 2002). The Shortnose Sturgeon is intermediate in hatchling and mature egg size, averaging 9.5 mm TL (0.37 inch) and 3.1 mm (0.12 inch) diameter, respectively (Dadswell 1979; Buckley & Kynard 1981). Investment in a greater amount of egg yolk produces hatchlings that are longer and heavier (Van Eenennaam et al. 2001; Deng et al. 2002). Lake Sturgeons have a wide range of hatchling sizes from 7–12 mm TL (0.27–0.47 inch). Within *Scaphirhynchus* both Pallid Sturgeon and Shovelnose Sturgeon hatchlings are 7–9 mm TL (0.27–0.35 inch) (Snyder 2002). Larval development and behavior are discussed in the morphology and behavior sections, respectively.

ECOLOGY

Habitat

Sturgeons inhabit fresh, brackish, and marine waters in North America. All three species of *Scaphirhynchus* spend their entire lives in large rivers, and Lake Sturgeons occur in large rivers or lakes (potamodromous) with adults occasionally entering brackish water. Adult Shortnose Sturgeons and White Sturgeons use brackish water (semi-anadromous or amphidromous), although a few individuals of Shortnose Sturgeon use marine habitat, and some populations of White Sturgeon are landlocked. Green Sturgeons and Atlantic Sturgeons move into the sea as adults (anadromous) using near-shore areas. All Sturgeons must spawn in fresh water (Bemis & Kynard 1997; Boreman 1997; Wilson & McKinley 2004). In general each phase of an adult's life history (spawning, post-spawning, non-spawning, overwintering, and feeding) and each life stage (embryo, larva, juvenile, and subadult) requires a different habitat (Auer 1996; Parsley et al. 2002). Potamodromous, semi-anadromous, and anadromous species differ greatly in habitat use for many of these life history phases or stages (Rochard et al. 1990).

Adult and subadult *Scaphirhynchus* inhabit the main channel, channel borders, or pools downstream of sand bars or wing dikes in large rivers in areas of moderate to high flows. They typically occur over sand but also are found over silt, gravel, rubble, and bedrock at depths from 0.9 to 10 m (3–32.8 feet) (usually 2–6 m, 6.6–19.7 feet) (Keenlyne 1997; Wilson & McKinley 2004; Gerrity et al. 2008). Pallid Sturgeons use sandy substrates, greater depths, wider river channels, and mid-channel bars more often than co-occurring Shovelnose Sturgeons (Bramblett & White 2001). Pallid Sturgeons prefer downstream island tips and areas between wing dams in the Mississippi River (Hurley et al. 2004b) compared with main channel habitat without islands in the Missouri River (Gerrity et al. 2008). Bottom current velocities and substrate appear to play a more important role in habitat selection than does depth (Quist et al. 1999).

The Lake Sturgeon inhabits large lakes and rivers usually at 4–9 m (13.1–29.5 feet) depth (≤43 m, 141 feet), over a variety of substrates including clay, mud, sand, gravel, and rock (Wilson & McKinley 2004). Greatest availability of food within a water body predicts habitat preferences (Rusak & Mosindy 1997). Semi-anadromous Sturgeons (White Sturgeons and Shortnose Sturgeons) can occupy large pools or deep channels in the main stem of rivers, the mouth of rivers in either freshwater or estuarine conditions, or near-shore marine environments from 3 to 30 m (9.8–98.4 feet) in depth, typically occurring over sand, gravel, and cobble (Kynard et al. 2000; Wilson & McKinley 2004). Anadromous species (Green Sturgeon and Atlantic Sturgeon) enter fresh water to spawn and generally remain in rivers after spawning (summer and early autumn) in deep holding areas (≤14 m), then return to salt water in the winter to feed (Erickson et al. 2002; Wilson & McKinley 2004; Heise et al. 2005), using shallow estuary and near-shore habitats typically over sandy substrate (Fox et al. 2002).

Summer holding areas are inhabited by both recently spawned and non-spawned adult and subadult anadromous species (Green Sturgeon and Atlantic Sturgeon) and are located downstream of spawning areas in the lower reaches of rivers that are still fresh water but may experience tidal influences. Sturgeons occupy deep areas over sand, clay, and gravel substrates; holding areas can average ≤28°C (82.4°F) in the South. In these habitats, individuals show little movement until migration to a marine environment occurs in autumn (Moser & Ross 1995; Sulak & Clugston 1999; Erickson et al. 2002; Heise et al. 2005). The Gulf Sturgeon does not feed while occupying summer holding areas (Mason & Clugston 1993), but nematodes, oligochaetes, and amphipods are found in the stomachs of adult and subadult Atlantic Sturgeons within these aggregation areas (Hatin et al. 2002). Coastal rivers are typically cooler than near-shore Gulf of Mexico waters

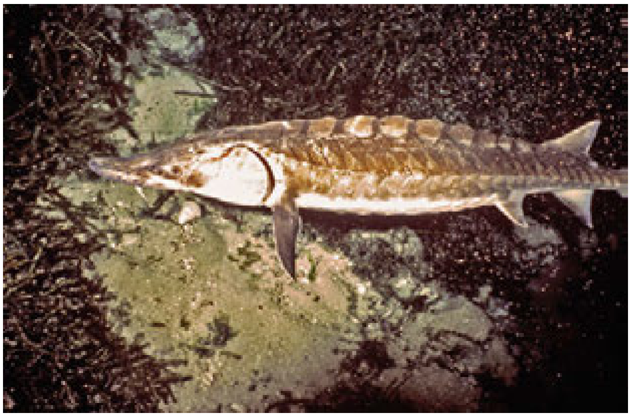

Figure 5.13. A Gulf Sturgeon, *Acipenser oxyrinchus desotol*, in Fanning Springs, Suwannee River drainage, Levy County, Florida, 26 May 1989 (photograph by and used with permission of Noel M. Burkhead).

in the summer and may act as thermal refugia, but specific holding areas are not cooler than surrounding river water and are likely selected for depth as refuge from high-velocity currents (Fig. 5.13) (Sulak & Clugston 1999; Hightower et al. 2002; Sulak et al. 2007). Some non-spawning adult and subadult Atlantic Sturgeons may remain exclusively in a marine environment for several years, including the summer (Bain 1997), and a few Gulf Sturgeons have remained in bays over the summer (Duncan et al. 2011). Green Sturgeons from all known spawning populations were detected in Willapa Bay estuary, Washington, during the summer when water temperatures exceed coastal water temperatures by ≥2°C (3.6°F), exhibiting rapid and extensive intra- and inter-estuary movement. Green Sturgeons are likely using this habitat for foraging; they are not present in the winter when water temperatures are 10°C (50°F) (Moser & Lindley 2007).

Overwintering habitat for adult potamodromous Sturgeons includes deep (>6 m, 19.7 feet), slower water for Lake Sturgeons (Rusak & Mosindy 1997) compared with shallow (1–2 m, 3.3–6.6 feet) channel crossovers with slow bottom flows for Shovelnose Sturgeons (Quist et al. 1999). Semi-anadromous species inhabit deep (10–27 m, 32.8–88.6 feet), lower saltwater estuaries and estuarine lakes (Wilson & McKinley 2004), but ripening females can overwinter in deep freshwater sites adjacent to spawning grounds (Dadswell 1979). Anadromous Sturgeons feed over the winter and this is reflected in their habitat use. For Gulf Sturgeons, males usually inhabit bays and estuaries, but females use near-shore marine habitat; both are found typically 2–6 m (6.6–19.7 feet) deep over sandy or shell hash substrate containing crustaceans, Lancelets, annelids, sand dollars, polychaetes, and small bivalves (Fox et al. 2002; Edwards et al. 2007; Ross et al. 2009; Parauka et al. 2011). Adult Green Sturgeons inhabit deeper near-shore Pacific waters typically at depths of 40–70 m (131–230 feet) (Erickson & Hightower 2007). Anadromous Sturgeons from mixed stocks can be found in the same areas of concentration, possibly due to prey concentrations (Edwards et al. 2007; Erickson & Hightower 2007; Laney et al. 2007; Lindley et al. 2008; Ross et al. 2009).

Ontogenetic Shifts in Habitat Use

Sturgeon embryos are attached to hard substrates, including gravel, cobble, boulders, hard clay, and bedrock, in fast-flowing water at the spawning site. Depths vary from 0.6 to 13 m (2 to 42.7 feet) (Fox et al. 2000; Wilson & McKinley 2004). Upon hatching larvae of some species may remain at the spawning site, while others may relocate downstream (Kynard et al. 2002a; Kynard & Horgan 2002a; Kynard & Parker 2005).

Green Sturgeon larvae initiate downstream migration shortly after exogenous feeding begins, and laboratory studies indicate that habitat with slate-rock increases foraging effectiveness and growth rate and reduces mortality compared with sand and especially cobble substrate (Nguyen & Crocker 2007). Juvenile Green Sturgeons spend 1–4 years in freshwater and estuary habitats before entering the marine environment (Beamesderfer et al. 2007). Subadults use shallow regions of the San Francisco Bay estuary <10 m (32.8 feet) deep and occur over a wide range of temperature, salinity, and dissolved oxygen (Kelly et al. 2007).

Collection of early life stages of White Sturgeons indicates that yolk-sac larvae are transported from spawning areas into deeper areas with lower water velocities and finer substrates. Young-of-the-year individuals occur at depths of 9–57 m (29.5–187 feet) at slower velocities over hard clay, mud, silt, sand, gravel, and cobble. Juveniles occupy rivers at depths of 2–58 m (6.6–190.3 feet) at higher velocities over hard clay, mud, silt, sand, gravel, cobble, boulder, and bedrock (Parsley et al. 1993).

Juvenile Shortnose Sturgeons use the lower reaches of rivers, aggregating and intensively using areas <1 km (0.62 mile) in length on or near the bottom at depths of 2.1–13.4 m (6.9–44 feet). These areas are in fresh water when temperatures are >22°C (72°F) and in brackish waters (mean 5.4 ppt salinity) at cooler temperatures (Collins et al. 2002).

Atlantic Sturgeon juveniles use the fresh water near the saltwater wedge in estuary habitat near the channel at 6–10 m (19.7–32.8 feet) depths with low current over sand, silt, and clay substrate (Hatin et al. 2007b). Juvenile Atlantic Sturgeons use near-shore marine habitat 9.1–21.3 m (29.9–69.9 feet) deep over sand substrate (Laney et al. 2007), and juvenile Gulf Sturgeons use river mouths and nearby estuaries, only entering open high-salinity Gulf waters after a dramatic drop in air and water temperatures (Sulak et al. 2009).

In the Mississippi River smaller age-0 Pallid Sturgeons and Shovelnose Sturgeons (<50 mm TL, 2 inches) were collected at downstream tips of islands often over heavy detritus and in island side-channels and channel-border dikes, with few age-0 *Scaphirhynchus* of any size occupying the main channel. Mesohabitat included slow current near 0.1 m/s (0.3 foot/s), moderate depth of 2–5 m (6.6–16.4 feet), and a sand substrate (Hrabik et al. 2007; Phelps et al. 2010a). In the lower Missouri River age-0 *Scaphirhunchus* were associated with channel sandbars and dikes with relatively fast bottom current of 0.5–0.7 m/s (1.6–3.0 feet/s) (Ridenour et al. 2011).

Diet

All Sturgeons are carnivores in all life stages, switching from zooplankton as larvae to benthic invertebrates and fishes as juveniles and adults (Tables 5.1 and 5.2). Early life stages have more restricted diets relative to older life stages. Larval and young-of-the-year White Sturgeons (1.5–29 cm TL, 0.6–11.4 inches) feed primarily on amphipods, but also consume copepods and dipteran larvae and pupae (Muir et al. 2000). Young-of-the-year Shovelnose Sturgeons feed exclusively on dipteran and ephemeropteran larvae (Braaten et al. 2007).

Most juvenile and adult Sturgeons are opportunistic predators that use a wide variety of benthic organisms over diverse substrates. All *Scaphirhynchus* feed on a variety of aquatic insects as well as snails, mussels, crayfishes, fish eggs, and occasionally fishes with Pallid Sturgeons transitioning to a mostly piscivorous diet (mostly chubs, Cyprinidae, Carps and Minnows, but also darters, Percidae, Perches) as juveniles (average 53.8 cm FL, 21.2 inches and 518 g, 1.15 pounds) and adults. Adult Alabama Sturgeons also consume significant amounts of fish, an average of 34.5% of the diet by volume (Carlson et al. 1985; Wilson & McKinley 2004; Gerrity et al. 2006; Hoover et al. 2007; Keevin et al. 2007; Grohs et al. 2009; Rapp et al. 2011). Species of *Acipenser* also consume diverse prey, including nematodes, oligochaetes, amphipods, aquatic insects, mollusks (including the invasive Zebra Mussel), crayfishes, and fishes in fresh water and mysids, copepods, polychaetes, decapods, and fishes in brackish and marine waters (Hatin et al. 2002; Jackson et al. 2002; Wilson & McKinley 2004; Savoy 2007). The diet of Atlantic Sturgeons in age-0, juvenile, and subadult stages appears to be more specialized relative to the more diverse diet of sympatric Lake Sturgeons (Guilbard et al. 2007).

Feeding Periodicity, Seasonality, and Fasting

Adult anadromous species typically feed little or not at all in fresh water in the summer and early autumn, followed by high levels of feeding in the winter and early spring (Sulak & Randall 2002), but variability exists even within a species. Gulf Sturgeons do not feed while occupying summer holding areas and lose about 12% of their weight (Mason & Clugston 1993; Carr et al. 1996), but nematodes, oligochaetes, and amphipods are found in the stomachs of adult and subadult Atlantic Sturgeons within these aggregation areas (Hatin et al. 2002). In northern populations of the semi-anadromous Shortnose Sturgeons fasting occurs in winter and early spring while in fresh water, but individuals in saline water feed all year (Dadswell 1979; Kynard 1997; Kynard et al. 2000). The potamodromous Shovelnose Sturgeon likely does not actively feed during the winter in the Kansas River, Kansas (Quist et al. 1999), but in the middle Mississippi River the number of prey items in Shovelnose Sturgeon stomachs was highest in the winter and spring and lowest during summer and autumn in concert with high temperatures and low discharge (Seibert et al. 2011). This is supported by both Shovelnose Sturgeons and Pallid Sturgeons being readily collected on trotlines baited with worms in the Mississippi River in winter, peaking at 10°C with practically no Sturgeons collected at temperatures >20°C (Killgore et al. 2007).

Seasonal shifts in feeding behavior in juvenile and adult species of *Scaphirhynchus* are reflective of the location and availability of prey items and the corresponding river flow rates. During autumn months Shovelnose Sturgeons use the major components of invertebrate drift, which constitutes a major portion of the biomass available. As drift decreases in the winter, Sturgeons prey on a more diverse array of aquatic and terrestrial invertebrates. In spring and summer Sturgeons forage almost exclusively on benthic invertebrates (chironomid midges) as river discharge rates increase (Modde & Schmulbach 1977).

Fasting in Sturgeons often spans seasons of highest or lowest water temperatures followed by shorter periods of intense feeding (Sulak & Randall 2002). Anadromous species enter fresh water to spawn and some (Green Sturgeon and Atlantic Sturgeon) remain in deep holding areas during summer and early autumn before returning to salt water in winter to feed; Gulf Sturgeons suspend feeding entirely in these aggregation areas (Moser & Ross 1995; Sulak & Clugston 1999; Erickson et al. 2002; Hatin et al. 2002; Heise et al. 2005; Sulak et al. 2007). Conversely, fasting occurs while in fresh water in winter and early spring in northern populations of the semi-anadromous Shortnose Sturgeon (Dadswell 1979; Kynard 1997). All fishes have indeterminate growth, which is pronounced in ancient fish taxa, including Sturgeons, but functional and ecological limits to body size for riverine species and fasting may keep Sturgeons below these limits. Examples include limiting body size to allow navigation of shallow shoals and rapids and avoid the depletion of limited riverine prey biomass by not exploiting this resource. Fasting leads to adult males with near-constant ultimate sizes in many *Acipenser* species; females continue to grow slowly, probably to accommodate more egg mass (Sulak & Randall 2002).

Competition and Resource Partitioning

Competition between North American Sturgeon species is possible along either coast or within the Mississippi River basin. Only when species occur in relatively similar abundances can potential resource partitioning be examined. The Shortnose Sturgeon and Atlantic Sturgeon can co-exist in similar numbers in Atlantic Slope rivers, and they share many life history attributes. In the Merrimack River and estuary, Massachusetts, these two species used different habitats (except for a saline reach of the river in the spring), perhaps to minimize competition (Kieffer & Kynard 1993). In contrast, the two species are not spatially segregated for large parts of their life histories in the Hudson River and estuary, New York and New Jersey, with similar-sized individuals of both species co-occurring in the same habitats (Bain 1997). In the St. Lawrence estuary transition zone, Atlantic Sturgeons and Lake Sturgeons co-occur, yet diet overlap is low with Atlantic Sturgeons primarily feeding on prey within the substrate and Lake Sturgeons consuming prey on or near the substrate (Guilbard et al. 2007). In a laboratory setting, large individuals (average 10.6 cm TL, 4.2 inches, and 9.6 g, 0.34 ounce) of Shortnose Sturgeons were dominant over small conspecifics (average 6.1 cm TL, 2.4 inches, 4.8 g, 0.17 ounce) when competing for limited foraging space (Kynard & Horgan 2002a). Species-specific differences in peak activity levels in co-occurring *Scaphyrinchus* also is suggestive of temporal resource partitioning (Curtis et al. 1997; Bramblett & White 2001).

Age and Growth

Annular rings in numerous hard structures (clavicles, cleithera, fulcra, subopercles, scutes, sphenoids) are used to discern growth patterns and age Sturgeons, but the most common structure used is a section of the pectoral fin ray that can be removed without mortality and gives the most reliable age estimate (Cuerrier 1951; Brennan & Cailliet 1989; Stevenson & Secor 1999; Jackson et al. 2007). An opaque band is laid down in the summer and a translucent band in the winter, but this pattern can vary (Brennan & Cailliet 1989; Whiteman et al. 2004). Most validation studies using marked and known-aged fish in species of *Acipenser* and *Scaphirhynchus* indicate this method has low accuracy and precision with ages typically underestimated, especially for older Sturgeons. Underestimation of age in turn can lead to overestimation of growth and mortality (Rien & Beamesderfer 1994; Rossiter et al. 1995; Hurley et al. 2004a; Whiteman et al. 2004).

Regardless of the inaccuracy of aging, Sturgeons are among the longest-lived fishes. The oldest reported Sturgeon was a 154-year-old Lake Sturgeon (94.3 kg, 208 pounds) (Scott & Crossman 1973). A 104-year-old White Sturgeon (280 cm FL, 110 inches) was the only other North American Sturgeon over the century mark (Rien & Beamesderfer 1994). Maximum age for other species of *Acipenser* ranges from 53 to 67 years (Cech & Doroshov 2004; Pikitch et al. 2005; Beamesderfer et al. 2007) and species of *Scaphirhynchus* range from 41 to 43 years old with southern populations living only half as long (Keenlyne & Jenkins 1993; Everett et al. 2003; Killgore et al. 2007). In all Sturgeons, females attain greater age (and size) than do males due to their later maturity and longer lifespan (Van Eenennaam et al. 2006). Importantly, most maximum or older ages are represented by few individuals in a population; most individuals within a species are much younger than the maximum (Sulak & Randall 2002). Therefore, the traditional paradigm of female Sturgeons typically reaching a great age and having multiple spawning events over their lifetime is incorrect; most Sturgeon populations are dominated by young adults. A census from 1986–1999 for a population of the Gulf

Sturgeon in the Suwannee River, Florida, indicated the maximum age was 20–25 years (2.1–2.2 m TL or 6.9–7.2 feet, ≤90 kg or 198 pounds), but the older Sturgeons made up <0.5% of the population, which was dominated by 8- to 16-year-olds (Sulak & Randall 2002).

Sturgeons grow relatively slowly, which is typical for large, long-lived fishes (Stevenson & Secor 1999; LeBreton & Beamish 2004). Growth is fastest for young Sturgeons but slows as they get older and larger; most early growth is represented by gain in length that switches to most growth as weight in adults (Kallemeyn 1983; Secor et al. 2000; LeBreton & Beamish 2004). Green Sturgeons grow to 30 cm (11.8 inches) in their first year but slow to 7–10 cm/year (2.8–3.9 inches/year) through age 10 (Beamesderfer et al. 2007). Absolute growth rates for Pallid Sturgeons in the Missouri River basin range between 0.39 and 1.18 mm/day (0.02–0.05 inch/day) for age 1 but only 0.01 to 0.27 mm/day (≤0.01 inch/day) for age 2–6 (Shuman et al. 2011). Young-of-the-year Shovelnose Sturgeons grow at 0.44–2.95 mm/day (0.02–0.12 inch) in the upper Missouri River with higher growth rates for earlier spawned cohorts (Braaten & Fuller 2007; Ridenour et al. 2011). Similar growth rates of 0.82–2.18 mm/day (0.03–0.09 inch) are reported for age-0 *Scaphirhynchus* spp. in the Mississippi River (Phelps et al. 2010b). Much faster growth rates and earlier maturation occur among different-sized species with the smaller Shovelnose Sturgeons growing three to five times faster than and maturing in half the time of the Shortnose Sturgeon or White Sturgeon (Morrow et al. 1998a). Males typically reach sexual maturity earlier than females, but females live longer and therefore grow to a significantly larger size. This pattern can be realized through faster growth rates for males (Dadswell 1979; Stevenson & Secor 1999), but equal growth rates are observed for both sexes (Bruch 1999), or females can grow faster than males (Bain 1997).

Food (quantity and quality) and temperature are the two main controlling factors influencing growth in all fishes, including Sturgeons (LeBreton & Beamish 2004). Fast growth occurs for anadromous Sturgeon species when subadults transition into adults and move into a marine environment or when semi-anadromous juveniles enter lower rivers at the interface of fresh and salt waters. The fast growth is due to the rich benthic invertebrate resources available in these habitats relative to freshwater systems and the high energy cost of foraging in a lotic environment (Kynard 1997; Sulak & Randall 2002). Adult Gulf Sturgeons lose on average 12% of their body weight while in riverine habitats, but can gain 20% while foraging in the Gulf of Mexico (Carr et al. 1996). Growth rates for Sturgeons are low when dams block migration to these marine environments (DeVore et al. 1995; Kynard 1997) or decrease productivity by altering downstream and upstream habitats (McKinley et al. 1993; Beamesderfer et al. 1995; Everett et al. 2003). As in most fishes, warmer temperatures also increase growth rates for Sturgeons. A general trend of increased growth with decreasing latitude attributed mostly to increasing temperatures has been noted in the Lake Sturgeon (Fortin et al. 1996; Power & McKinley 1997; Noakes et al. 1999), Shortnose Sturgeon (Kynard 1997), and Atlantic Sturgeon (Secor et al. 2000; Stevenson & Secor 1999); associated with this increased growth rate is earlier maturation and smaller maximum sizes. This pattern is not observed consistently in *Scaphirhynchus* (Morrow et al. 1998a; Everett et al 2003; Kennedy et al. 2006), but Shovelnose Sturgeons in the upper Missouri River are generally larger than Mississippi River individuals and are heavier for a given length (Quist et al. 2002). Temperature also contributes to growth rates at the population level. Faster growth was observed in a population of White Sturgeons that has higher year-round water temperatures due to an influx of spring water (Cochnauer et al. 1985).

Other factors can cause decreased growth in Sturgeons. Most species of Sturgeons are oxygen conformers and demonstrate a reduced metabolic rate at lower oxygen levels (Singer & Ballantyne 2004; Burggren & Randall 1978; see physiology section) that can lead to decreased growth at non-lethal levels of hypoxia (Secor & Gunderson 1998).

Population Sizes, Densities, and Productivity

All species of Sturgeons now are fragmented, and populations have declined from historical levels. The size and density of populations within a given species can vary greatly. Estimates of abundance of Shovelnose Sturgeons vary from 2,500 fish/km (4,023 fish/mile) in an unchannelized segment of the Missouri River to only 1,030 fish/km (1,658 fish/mile) for the navigation-altered Mississippi River down to 100 fish/km (161 fish/mile) in the small Red Cedar River, Wisconsin (Keenlyne 1997). Abundance estimates of White Sturgeons in the lower Columbia River declined from 895,500 adults at a density of 14.6 fish/ha (5.9 fish/acre) in the unimpounded reach to 6,300–51,400 adults at densities of 0.3–6.2 fish/ha (0.12–2.5 fish/acre) in impounded areas (Beamesderfer et al. 1995; DeVore et al. 1995). Population estimates for Lake Sturgeons range from only 33 individuals in a river system up to 34,000 fish (Wilson &

McKinley 2004). Some species show distinct regional variation in abundance; Shortnose Sturgeons number 38,000 in the Hudson River, New York, and 18,000 in the St. John River estuary, Canada, compared with <1,000 in Georgia rivers (Dadswell 1979; Bain 1997; Kynard 1997). Gulf Sturgeon population estimates range from 292 age-2 or older individuals in the Pearl River, Louisiana and Mississippi, 500–911 total individuals in the Yellow River, Florida, and ≤7,650 Sturgeons >60 cm TL (23.6 inches) and older than age 2 in the Suwannee River, Florida (Morrow et al. 1998b; Sulak & Clugston 1999; Berg et al. 2007).

Dams can have dramatic negative effects on *Scaphirhynchus*. In the highly fragmented Missouri River basin, a population of non-reproducing Pallid Sturgeons in the lower Yellowstone and upper Missouri Rivers numbered 158 wild adults in 2004, down from an estimated historical population of ≤968 adults (Braaten et al. 2009b). The species with the lowest population size in North America by far is the Alabama Sturgeon with dams as one of the main factors in reducing the population to barely detectable levels (see conservation section; Mayden & Kuhajda 1997a; USFWS 2000; Rider & Hartfield 2007).

Natural mortality in Sturgeons is low relative to that of many other fishes with natural annual mortality rates of 7–12% for most adult *Acipenser* (DeVore et al. 1995; Boreman 1997). One population of protected Gulf Sturgeons had a low natural mortality rate of 11.9%, but higher rates of 16–34% in other populations may reflect mortality due to bycatch in the Gulf of Mexico (Morrow et al. 1998b; Sulak & Clugston 1999; Pine et al. 2001; Berg et al. 2007). Mortality is much higher (18–25%) in juvenile and subadult *Acipenser* (Beamesderfer et al. 1995; Pine et al. 2001) except for subadult Green Sturgeons, which have a rate of 14% (Beamesderfer et al. 2007). Annual mortality rates in exploited populations of Sturgeons range from 14 to 37% in *Acipenser* to 20% in Shovelnose Sturgeons (Beamesderfer et al. 1995; DeVore et al. 1995; Morrow et al. 1998a; Bruch 1999; Beamesderfer et al. 2007).

Because of their comparatively low mortality as adults and perceived longevity, Sturgeon populations often are considered relatively stable, and this can be reinforced by studies that show stable numbers of total individuals with periodic sampling. But studies showing population structure by size or age often indicate that populations are dynamic and unstable with periodic successful year-classes interspersed with unsuccessful year-classes (Sulak & Randall 2002). Unstable population structure is observed in the Gulf Sturgeon (Sulak & Clugston 1999), Lake Sturgeon (Noakes et al. 1999; Craig et al. 2005), and White Sturgeon (Kohlhorst et al. 1991) and appears to be a typical feature of Sturgeon life histories (Sulak & Randall 2002). Population structure studies need to include the sex of individuals because females are larger and older than males and bimodal peaks may represent differences in size and age of sexes (Van Eenennaam et al. 2006) rather than year-class strengths.

Predation

Other than humans, adult Sturgeons have few if any predators, but this is not the case for early life stages. Sturgeon eggs and larvae are preyed on by a variety of fishes as well as crayfishes (*Orconectes* spp.) and the Mudpuppy (*Necturus maculosus*) (Kempinger 1988; Miller & Beckman 1996; Nichols et al. 2003). Altered river conditions caused primarily by dams can lead to increased predation of Sturgeon eggs and larvae because of reduced cover from scoured river bottoms and reduced sediment loads and turbidity from tailwater releases (i.e., sediments are trapped behind dams) (Gadomski & Parsley 2005a). But predation of eggs and larvae at a spawning site for Shortnose Sturgeons was low in the Connecticut River with the stomach of only 1 of 40 potential predators containing Sturgeon eggs (Kynard & Horgan 2002a). Juvenile Sturgeons may not be highly susceptible to predation because of their sharp scutes and spines, benthic habitat, and fast growth (Parsley et al. 2002). The vulnerability of age-0 Pallid Sturgeons <100 mm TL (3.9 inches) to predation by Channel Catfish (*Ictalurus punctatus*) and Smallmouth Bass (*Micropterus dolomieu*) was considered low in a laboratory setting especially when alternative prey was present (French et al. 2010), but similar-sized White Sturgeons were preyed on extensively by Prickly Sculpins (*Cottus asper*) and Northern Pikeminnows (*Ptychocheilus oregonensis*) even with alternative prey in laboratory trials (Gadomski & Parsley 2005b).

Parasites

Information on parasites in North American Sturgeons is only available for about half of the species, yet a fairly diverse assemblage is known. These include fungi (2 species), protozoa (1), jellyfish (2), flukes (20), tapeworms (2), nematodes (14), thorny-headed worms (4), leeches (8), and copepods (4). Parasites can occur in all Sturgeon life stages, including a jellyfish parasite (*Polypodium hydriforme*) that only parasitizes eggs (early pre-vitellogenic to mature) of Sturgeons and the Paddlefish (Hoffman 1999; Choudhury & Dick 2001; Raikova 2002). Similar parasites occur in other Sturgeons in Asia (Choudhury & Dick 2001; Bauer et al. 2002). Historical patterns among species of Sturgeons are often reflected in small, highly distinct monophyletic parasite lineages, and some parasites are only found on closely related Sturgeon species, such as the fluke *Diclybothrium armatum* that is only present in the sister-species Shortnose and Lake Sturgeons (Choudhury & Dick 1996, 2001). Parasites can also invade the genes of Sturgeons. Strong evidence indicates a fluke in the genus *Schistosoma* has horizontally transferred some genes into the Lake Sturgeon genome (Hale et al. 2010).

Other organisms parasitize Sturgeons but are not typically considered in the parasite literature. The iridovirus is a species-specific pathogen of wild White Sturgeons, but the virus has caused excessive mortality in hatcheries for this species and for the Pallid Sturgeon and Shovelnose Sturgeon (MacConnell et al. 2001; Kurobe et al. 2008). Larval mussels (glochidia) must attach to and parasitize fishes to metamorphose into juveniles. The Hickorynut Mussel (*Obovaria olivaria*) only uses Shovelnose Sturgeons and Lake Sturgeons as hosts; this mussel co-occurs in the large-river habitats with Shovelnose Sturgeons and in Great Lakes drainages with Lake Sturgeons (Howard 1914a; Coker et al. 1921; Brady et al. 2004; Zanatta & Woolnough 2011). The Shovelnose Sturgeon, along with other fish species, is naturally infested by glochidia of the Pimpleback (*Quadrula pustulosa*) and the Yellow Sandshell (*Lampsilis teres*), but transformation of either mussel species was not observed (Surber 1913; Wilson 1916; Coker et al. 1921). Similarly, the Atlantic Sturgeon was artificially infected in a laboratory with glochidia of the host-generalist Creeper (*Strophitus undulatus*), but encysted glochidia did not transform to juveniles (Van Snik Gray et al. 2002). Parasitic Lampreys use the Lake Sturgeon, Atlantic Sturgeon, and White Sturgeon as hosts and may kill even large Sturgeons; ≤27 individual Lampreys have been removed from a single Sturgeon (Scott & Crossman 1973; Becker 1983; Scott & Scott 1988). Silver Lampreys (*Ichthyomyzon unicuspis*) are the predominant species that attach to Lake Sturgeons, and ≤70% of individuals in a population can possess fresh Lamprey marks. Large Lake Sturgeons tend to have more wounds or fresh scars (Thomas & Haas 2002; Cochran et al. 2003).

CONSERVATION

Sturgeons possess a combination of morphology, habits, and life history characteristics that make them highly vulnerable to anthropogenic activities, especially those that block migratory routes, destroy essential habitat, and harvest adults (Rochard et al. 1990; Boreman 1997; Wilson & McKinley 2004). This vulnerability has led to small remnant populations that are slow to recover in most species even with regulated harvest and habitat improvement, and therefore, almost all Sturgeons worldwide are considered Imperiled (Birstein 1993; Auer 2004). In the United States, the Pallid Sturgeon, Alabama Sturgeon, Shortnose Sturgeon, and a population of the White Sturgeon (Kootenai River) are protected under the U.S. Endangered Species Act as Endangered, and four of five distinct population segments (DPS) of the Atlantic Sturgeon (New York Bight, Chesapeake Bay, Carolina, and South Atlantic) are proposed as Endangered. Gulf of Maine DPS for the Atlantic Sturgeon, the southern DPS for the Green Sturgeon (Sacramento River, California), and all populations of Gulf Sturgeons are considered Threatened (Auer 2004; Wilson & McKinley 2004; NMFS 2006, 2010ab). Shovelnose Sturgeons are also considered Threatened in areas where they are sympatric with the Endangered Pallid Sturgeon due to similarity of appearance. Areas of sympatry include most of the Missouri River to its mouth, the Mississippi River from just above the mouth of the Missouri River to its mouth, the Atchafalaya River, and the lower reaches of several larger tributaries (USFWS 2010a). The Committee on the Status of Endangered Wildlife in Canada considers the White Sturgeon as Endangered; several populations of Lake Sturgeons as Endangered, Threatened, or of Special Concern; the Atlantic Sturgeon as Threatened; and the Shortnose Sturgeon and Green Sturgeon as of Special Concern (COSEWIC 2011). Even though other populations of North American Sturgeons do not have federal protection, they are all considered at least Vulnerable (Warren et al. 2000; Auer 2004; Wilson & McKinley 2004; Jelks et al. 2008), and the Alabama Sturgeon is considered Critically Endangered and on the brink of extinction due to its limited range of only 524 km (326 miles) in the Alabama and Cahaba Rivers of the Mobile Basin and its extreme rarity. Only 5 individuals were captured in an 8-year period despite >2,447 person-days of effort covering >200 river km (124 miles) (Mayden & Kuhajda 1997a; Rider & Hartfield 2007; USFWS 2009; IUCN 2011).

All North American *Acipenser* species occur in both U.S. and Canadian waters, and the Gulf Sturgeon, Pallid Sturgeon, and Shovelnose Sturgeon range across numerous states. These wide-ranging distributions across multiple political boundaries can result in varying and opposing management strategies (Rasmussen 1999; Léonard et al. 2004). Even when multijurisdictional organizations are formed they may not be effective. For example, the Mississippi Interstate Cooperative Resource Association (MICRA) has no regulatory authority and only limited intergovernmental influence overseeing Sturgeons and the Paddlefish in the Mississippi River basin (Graham & Rasmussen 1999; Rasmussen 1999; Williamson 2003). With the worldwide interest in Sturgeon products, especially caviar, and the sharp decrease in catch globally, international management of Sturgeons is essential and is performed under the Convention on International Trade of Endangered Species (CITES). The authority of CITES, however, is limited being based on the voluntary participation of >160 countries to control international trade (Raymakers & Hoover 2002; Léonard et al. 2004; Pikitch et al. 2005). Under CITES, all Acipenseriformes are listed as Appendix I (threatened with extinction) or Appendix II species (uncontrolled trade might threaten their existence) that require permits and certifications for international trade involving Sturgeons and the Paddlefishes along with additional initiatives for their protection, especially against illegal trade (Raymakers & Hoover 2002; Léonard et al. 2004).

Artificial Propagation and Stocking

With coastal Sturgeon fisheries in North America currently regulated, the lack of recruitment in extant populations and reestablishment of extirpated populations are the main obstacles facing Sturgeon recovery (Secor et al. 2002; Coutant 2004). Lack of recruitment stems from a historical reduction of spawning adults, reduction or loss of cues (temperature and flow) to initiate proper egg production and spawning migrations, limited access to or lack of quality spawning habitat, and improper conditions and habitats for embryos and larvae to develop and grow (Parsley et al. 2002). As such, a main tool used to recover Sturgeon populations and species is the stocking of hatchery-reared specimens that can bypass these recruitment constraints and produce stock for reintroduction into historical habitats. But consideration must be given to intraspecific genetic variation in natural populations due to fidelity for spawning sites, maintaining genetic diversity within wild populations, and the release of progeny that are free of disease and can adapt from a hatchery to a natural setting. Ultimately habitat restoration must occur to address recruitment failure (Andreasen 1999; Auer 2004; Pikitch et al. 2005). Reintroduction efforts are ongoing for all species of North American Sturgeons except the Alabama Sturgeon (Rider & Hartfield 2007; Koch & Quist 2010). Successful reintroductions include fast growth rates for hatchery-reared Lake Sturgeons reintroduced into a New York lake with potential spawning habitat available to allow for a self-sustaining population (Jackson et al. 2002), the reestablishment of an extirpated population of Lake Sturgeons in a Wisconsin river via stocking and adult translocation (Runstrom et al. 2002), hatchery-reared juveniles of the endangered population of Kootenai White Sturgeons becoming established (Ireland et al. 2002), and the successful reintroduction of hatchery-reared endangered Pallid Sturgeons in a riverine section of the upper Missouri River isolated by dams and reservoirs (Jordan et al. 2006; Shuman et al. 2011). Other populations of extant Pallid Sturgeons in the Missouri River with little or no natural recruitment for >20 years due to lack of proper habitat are being successfully augmented with hatchery-reared progeny to avoid extirpation (Gerrity et al. 2008; Braaten et al. 2009b; Steffensen et al. 2010; Shuman et al. 2011). Hatchery-reared Shortnose Sturgeons (both fertile and sterile) have the same seasonal movements and microhabitat selection as wild individuals, indicating that hatchery Sturgeons can be integrated into wild populations and can be used as surrogates for behavioral studies (Trested et al. 2011). Most of these reintroductions are too recent to determine if these populations will become self-sustaining. Unfortunately stocking has also created potential problems for imperiled Sturgeons. Numerous hatchery-reared Shortnose Sturgeons released in the Savannah River, North Carolina and Georgia, have been found in other river systems that could disrupt genetic structure in distinct populations (Smith et al. 2002b). Shortnose Sturgeons within the Edisto River system, South Carolina, have depressed genetic diversity that may be due to former stocking programs not capturing genetic diversity in released progeny (Quattro et al. 2002). The source population is critical even in reintroductions into recovered habitat. Hatchery-reared Lake Sturgeons from Lake Winnebago stock moved rapidly downstream and out of the target area in the Menominee River, but native translocated riverine Lake Sturgeons stayed in the intended area (Thuemler 1988). Overstocking can potentially exceed contemporary carrying capacity. A Pallid Sturgeon augmentation program in the upper Missouri River targeted 1,700 adults and predicted adult number may reach 3,900 by 2038, but historical abundance estimates indicate a maximum of 968 adults (Braaten et al. 2009b). These problems can be minimized by developing peer-reviewed stocking plans that address imprinting and genetic diversity issues inherent to any hatchery program (Smith et al. 2002a; Ludwig 2006; George et al. 2009).

For species that lack female brood stock for an artificial propagation program, fully viable androgenic nuleocytoplasmic hybrids were produced in Eurasian endangered Sturgeons. This was accomplished by inactivation of the egg nuclei from a donor species, dispermic fertilization using sperm from the imperiled species, and heat shock to the embryo to enhance fusion of male pronuclei to form a diploid individual. Because sturgeon eggs have numerous micropyles, simultaneous penetration of two spermatozoa is possible. The progeny have the nuclear DNA of the paternal species and the mtDNA of the maternal species. If sperm are from two different males the level of heterozygosity is similar to that of typical hybrids. Expression of morphological characters varies with development, with maternal effects expressed at 6 months and the final development of paternal characters at 1 and 3 years of age. Because the mechanism of sex determination in Sturgeons is unclear, it is unknown what sex ratios would be realized. The use of cryopreserved sperm is successful, but with a decreased rate of fertilization and survival. Viable progeny have only been produced between species with the same ploidy level (Grunina & Recoubratsky 2005; Grunina et al. 2006, 2009).

Habitat Restoration

The creation of artificial spawning grounds can produce successful hatching provided the structures are placed at the proper depth and current velocity, have adequate surface area, consist of the appropriate substrate size, and have sediment-free interstitial spaces that are maintained. Artificial spawning habitat was successful for Lake Sturgeons in the St. Lawrence River, Michigan, and Des Prairies River, Ontario (Johnson et al. 2006b; Roseman et al. 2011; Dumont et al. 2011). Discrete choice modeling of gravid female Shovelnose Sturgeon habitat selection in the highly altered lower Missouri River indicated that restoration efforts need to concentrate on channel complexity because of the importance of variability in surrounding depths to gravid females (Bonnot et al. 2011).

Fisheries

Overfishing contributed greatly to the decline of North American Sturgeons in the late 1800s and during various periods in the 1900s, nearly causing the extinction of some species (Williamson 2003; Auer 2004; Wilson & McKinley 2004; see conservation section). Legal Sturgeon harvest persists today as commercial, sport, and subsistence fisheries for the Atlantic Sturgeon, Lake Sturgeon, White Sturgeon, Green Sturgeon, and Shovelnose Sturgeon (see commercial importance section). For all species of *Acipenser*, strict regulations are typically in place for sport and subsistence fisheries, including minimum size lengths, restricted open seasons, and quotas. Two Canadian provinces allow sportfishing for the Atlantic Sturgeon, but any harvest is illegal in the United States. Three provinces and three states have a sport harvest for the Lake Sturgeon, which includes spearing in some states. In 2000, >5,000 fish were harvested with hook and line in Ontario and >2,500 taken with spears in Wisconsin. An annual commercial harvest of 80 mt (88.2 tons) of the Lake Sturgeon over the last 10 years in the Quebec portion of the lower St. Lawrence River has been maintained due to restrictive regulations, close monitoring of the commercial catch, and periodic assessment of the population (Mailhot et al. 2011). Washington, Oregon, and California allow sportfishing for White and Green Sturgeons. Sportfishing for the White Sturgeon is popular in western Canada and the northwestern United States (Figs. 5.14 and 5.15). In the Columbia River and its tributaries, harvest peaked at 62,400 Sturgeons in 1987. With regulatory changes, the annual harvest was lowered and has ranged between 33,500 and 45,100 since 1992. Sportfishing for the less desirable Green Sturgeon is minimal with ≤100 harvested annually in the lower Columbia River since

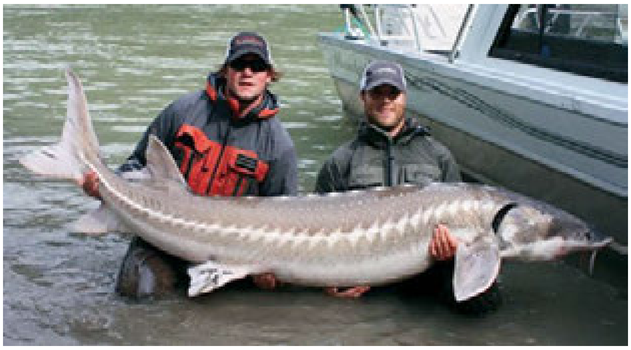

Figure 5.14. Because of their size, White Sturgeons, *Acipenser transmontanus*, are the focus of a popular, albeit somewhat specialized, sport fishery in portions of their range. This individual was caught, recorded, and released in the upper Fraser River, British Columbia (photograph by and used with permission of Kevin Estrada, Sturgeon Slayers, www.sturgeonslayers.com, "Catch-Record-Release").

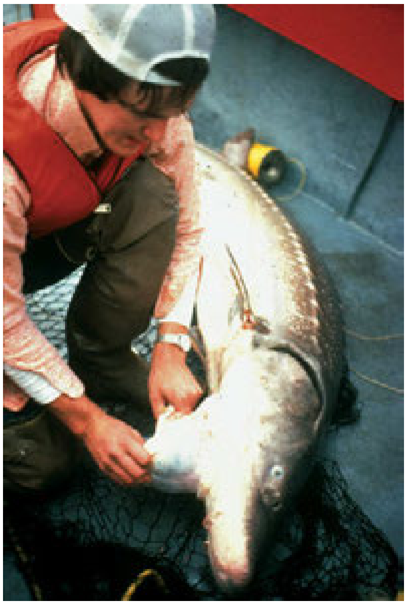

Figure 5.15. A White Sturgeon, *Acipenser transmontanus*, taken from the Columbia River, Washington. Note the protrusibility of the mouth (photograph by G. Burton).

1988, and total harvest declined from 6,494 annually in 1985–1989 to only 512 in 2003. Thirteen states permit sportfishing for the Shovelnose Sturgeon, but there is little oversight and restrictions are few and variable. Only one state enforces a season (Arkansas); five other states (Minnesota, Missouri, Montana, Nebraska, Wyoming) have creel or possession limits statewide, and no states maintain data on annual take. Regulations are inadequate (minimum length or harvest slot limit) in the commercial harvest of Shovelnose Sturgeons in all eight states where it is permitted, causing concern for the species due to the recent increase in demand and prices for North American caviar (Morrow et al. 1998a; Mosher 1999; Williamson 2003; Pikitch et al. 2005; Adams et al. 2007; Koch & Quist 2010). For example, declines occur in adult abundance, length, weight, and age of Shovelnose Sturgeons with increased harvest in the upper Mississippi River and with insufficient regulations in many states to maintain sustainable stocks (Colombo et al. 2007a; Koch et al. 2009c).

Commercial and sport fisheries targeting other fishes can negatively impact Sturgeons through incidental catch and bycatch. Fisheries for the American Shad (*Alosa sapidissima*), Goosefish (*Lophius americanus*), Dogfish Sharks (Squalidae), shrimp, and other species along the Atlantic Coast use gillnets, trawls, and pound nets that also are effective at capturing the endangered Shortnose Sturgeon and Atlantic Sturgeon, especially juveniles and subadults. Mortality estimates from bycatch range from 10 to 22% with another 20% injured (Collins et al. 1996, 2000b; Stein et al. 2004; Spear 2007); this is in addition to natural annual mortality rates of 7–12% for most adult *Acipenser* (DeVore et al. 1995; Boreman 1997). Annual bycatch mortality for Atlantic Sturgeons from Maine to North Carolina is estimated as 1,500 individuals/year, and 4.2 mt (4.6 tons) of bycatch of this species were reported in Canadian waters in 1998, although these statistics likely underestimate total losses (Williamson 2003; Stein et al. 2004; Kahnle et al. 2007). Bycatch is also a concern for the Green Sturgeon, including the threatened southern DPS, which is highly migratory along the Pacific Continental Shelf and overwinters in Canadian waters, where it is subject to intensive bottom trawl fisheries (Lindley et al. 2008). Even if mortality or injury is avoided, repeated capture and excessive handling by commercial fishers disrupt spawning migrations in Shortnose Sturgeons (Moser & Ross 1995). High mortality rates (16–17%) for the threatened Gulf Sturgeon in the Suwannee River, Florida, likely reflect death due to bycatch in the Gulf of Mexico (Sulak & Clugston 1999; Pine et al. 2001). In the Mississippi River, the endangered Pallid Sturgeon is similar in appearance to the sympatric and commercially harvested Shovelnose Sturgeon (Murphy et al. 2007a), and there are calls to ban all commercial fisheries for Sturgeons in the basin (Graham & Rasmussen 1999). Pallid Sturgeons have annual mortality rates of 11 and 30% downstream and upstream of the mouth of the Ohio River, respectively. The higher rate is attributed to Pallid Sturgeons being commercially harvested with Shovelnose Sturgeons, whose mortality rate in the upper Mississippi River upstream of the mouth of the Ohio River is 37% (Colombo et al. 2007a; Killgore et al. 2007). Direct evidence of bycatch of Pallid Sturgeons includes 2 of 113 total *Scaphirhynchus* spp. taken by commercial roe fishers even with observers on board, and an additional Pallid Sturgeon found dead in a retrieved ghost net (Bettoli et al. 2009a).

Because of the commercial value of Sturgeon products, especially caviar, illegal harvest of Sturgeons has and continues to be a threat to all species (Ludwig 2006). Sturgeons pursued for caviar are easy targets as they migrate in river systems and concentrate on spawning grounds, and protection can be difficult and costly because of the large distances Sturgeons travel (Auer 2004). North American species most affected by illegal harvest include Atlantic Sturgeon, Lake Sturgeon, White Sturgeon, and Shovelnose Sturgeon, and two endangered species, Shortnose Sturgeon and Pallid Sturgeon (Williamson 2003; Colombo et al. 2007a; Waldman et al. 2008b). Illegal take can be large. For example, a single poaching ring killed 2,000 adult White Sturgeons from the Columbia River to obtain 1,352 kg (2,981 pounds) of caviar over a 5-year period

(Cohen 1997). Recent advances in genetics allow differentiation of Sturgeon species from their caviar and flesh, which have given law enforcement agencies genetic forensic tools to identify protected species in the trade of Sturgeon commercial products (DeSalle & Birstein 1996; Birstein et al. 1999; Wolf et al. 1999; Congiu et al. 2002). But some species complexes are not readily identifiable with these forensic tools and data are lacking on identifying population-level variation, which is complicated in many instances by stocking programs that mix genotypes. Alternative molecular techniques such as single nucleotide polymorphism (SNP) markers may address some of these issues (Ludwig 2008; Waldman et al. 2008b). Aquaculture and wild-origin caviar can potentially be distinguished by examining fatty acid composition, but this would require the use of specific additives to formulated diets by aquaculturists (Gessner et al. 2008).

Dams

Unaltered free-flowing large river habitat was all but eliminated in the Northern Hemisphere in the 1900s, transforming rivers into a discontinuous series of large pools and deep runs (Sulak & Randall 2002). For Sturgeons, dams can negatively affect spawning migrations, quality and quantity of spawning habitat, embryo and larval development, genetic diversity, and growth.

All Sturgeons have upstream migrations associated with spawning, and dams obstruct these movements. Semi-anadromous and anadromous species typically have longer migrations and fewer spawning sites than potamodromous species and are therefore more susceptible (Cooke et al. 2002; Jager et al. 2007; Mora et al. 2009). Barriers to spawning areas can cause females to resorb eggs or not spawn. (Auer 1996). Disruption of natural flows downstream of dams can alter migratory cues for potential spawners (Mayden & Kuhajda 1997a). The presence of navigation locks may allow for limited upstream movement in Lake Sturgeons (Knights et al. 2002), but Shortnose Sturgeons do not use these as upstream passages (Cooke et al. 2002). Fish ladders can pass Sturgeons, even large White Sturgeons, but successful passage is limited and influenced by ladder construction (Parsley et al. 2007). A current velocity of 0.33m/s (1.1 feet/s) is sufficient to guide White Sturgeons to a horizontal ramp structure for dam bypass in a laboratory setting. An experimental flume at a 4% bed slope with baffles and average water velocities of 1.7–2.1 m/s (5.6–6.9 feet/s) representing the midsection of a fishway was capable of passing adult White Sturgeons, but field assessment of such structures, stress responses of Sturgeons, and their spawning success after ascent need to be examined (Cheong et al. 2006; Cocherell et al. 2011). Even if fishways are available for Sturgeons to bypass dams, upstream spawning sites may be inundated (Knights et al. 2002). If Sturgeons spawn above hydroelectric dams, post-spawning adults and any juveniles from successful spawns are at risk of entrainment and death on turbines during downstream migrations (Kynard & Horgan 2001; Jager et al. 2007).

Artificial lowering of spring and summer discharges from hydropower operations and for flood control reduces the availability and quality of spawning habitat for many Sturgeon species. For example, these actions buried cobble and gravel spawning sites for the Kootenai River White Sturgeon under fine sediments due to reduced velocities and shear stress. These effects are compounded by changes to channel morphology below dams (Rochard et al. 1990; Parsley & Beckman 1994; Paragamian et al. 2009). Controlled dam releases also can produce artificially high flows, which create high bottom velocities that preclude or reduce spawning (Buckley & Kynard 1985). Even if spawning is successful below dams, eggs may be laid in masses that have reduced survival from poor hatch success and increased predation and disease (Kempinger 1988; Auer 1996). Reduced flows can also lead to warmer water temperatures that negatively affect embryo development and hatching success (Van Eenennaam et al. 2005). Fluctuating water levels due to dam releases can dislodge embryos during high flows and expose and desiccate embryos during low flows (Kempinger 1988). Dams trap sediments and decrease turbidity, which may cause Sturgeons to use deeper and more restricted habitat for spawning and development of early life stages (Perrin et al. 2003) and likely increases predation on eggs and larvae (Gadomski & Parsley 2005a).

Larval Sturgeons can drift great distances below spawning sites as they grow and develop (e.g., Pallid Sturgeon drift for ≤530 km, 329 miles). Dams produce reservoirs with greatly reduced flow that may not provide habitat necessary for larval Sturgeons to survive, and multiple dams on a river often restrict riverine reaches to lengths too short for larval development (Auer & Baker 2002; Smith & King 2005a; Kynard et al. 2007; Braaten et al. 2008). Dams have dramatic negative effects on *Scaphirhynchus* with no documented recruitment for Pallid Sturgeons in the highly fragmented upper Missouri River basin for the past 35 years or for Alabama Sturgeons in the highly impounded Alabama River for decades (Mayden &

Kuhajda 1997a; USFWS 2000; Webb et al. 2005). For some river systems maintaining downstream reservoirs below maximum pool can increase the amount of riverine habitat (Gerrity et al. 2008).

Dams and altered habitat downstream of dams and within impoundments also affect genetics and growth of Sturgeons. Metapopulation modeling shows that multiple dams also restrict gene flow and hence genetic diversity within artificially segmented populations with upstream populations at risk of extirpation due to higher downstream and lower upstream migrations (Jager et al. 2001, 2007). Channelization and dredging of waterways in the riverine reaches above and below dams to allow for navigation also can destroy both river and estuary Sturgeon habitat (Burke & Ramsey 1995; Kynard 1997). Altered habitat below dams and within impounded areas can lead to slower growth rates for Sturgeons due to decreased productivity (McKinley et al. 1993; Beamesderfer et al. 1995; Everett et al. 2003).

Agriculture

Construction of levees to protect farmlands from winter and spring high water and the filling of isolated oxbows and backwaters to expand floodplain agriculture has led to the virtual elimination of riparian and backwater habitat in large-river ecosystems. Many rivers now are confined to narrow channels and cut off from the major source of organic nutrients. Sturgeons require this floodplain habitat for many important aspects of their life history, including feeding areas for all life stages and habitat for larvae and juveniles (USFWS 1993; Coutant 2004); year-class strength in Sturgeons is primarily dependent on survival in the first 2–3 months (Secor et al. 2002; Parsley et al. 2002). In addition, runoff from agriculture introduces numerous pollutants, including herbicides, pesticides, and fine sediments. For example, DDT occurred in tissues of Pallid Sturgeons 14 years after its ban in 1975 (Ruelle & Keenlyne 1993), and high silt loads on spawning substrates can lead to larval mortality in the Lake Sturgeon (Nichols et al. 2003).

Pollution

Sturgeons are affected by numerous forms of water pollution. They are susceptible to the accumulation of contaminants in their flesh and eggs because they are long-lived; ingest benthic organisms and organic material from the bottom of rivers, lakes, estuaries, and near-shore marine habitats; and have high lipid content (Auer 2004). Bioaccumulation of contaminants is exacerbated by the low capacity of Sturgeons to detoxify various compounds relative to other bony fishes (Singer & Ballantyne 2004). Instream cage studies on juvenile Shortnose Sturgeons to assess suitability of water quality in the Roanoke River led to a 91% mortality compared to only 0.6% mortality for the Fathead Minnow (*Pimephales promelas*), indicating that this standard toxicity test organism is an inappropriate surrogate for Shortnose Sturgeons in water quality or toxicity tests (Cope et al. 2011). Contaminants are introduced into aquatic systems from numerous sources such as mining, industry, urban discharge, and agricultural and urban runoff (Ruelle & Keenlyne 1993; Hinton 1998).

Given the imperiled status of Sturgeons, surprisingly few studies have examined the effects of pollutants, but the fact that they are imperiled restricts the collection of tissues for such studies (Auer 2004; Singer & Ballantyne 2004). Limited studies do show that Sturgeons accumulate heavy metals and organic chemicals (e.g., PCBs, DDT, and chlordane) that may lead to developmental and behavioral abnormalities and interfere with reproduction; concentrations within Sturgeons increase with age (Ruelle & Keenlyne 1993; MacDonald et al. 1997; Doyon et al. 1999; Alam et al. 2000; Auer 2004). Heavy metals and detergents impair olfactory sensory abilities (Kasumyan 2002), and sediment pollutants may place stress on the overall viable reproduction of Sturgeons (Kruse & Scarnecchia 2002). Elevated concentrations of organochlorines in intersexual and male Shovelnose Sturgeons with limited reproductivity (low gonad somatic index, GSI) were restricted to the brain-hypothalamus-pituitary complex. This indicates these pollutants alter hormone production and reception necessary for proper gonadal development (Koch et al. 2006). Intersexuality rates in Shovelnose Sturgeons are 2 to 7.5% based on examination of gonads and the use of sexually dimorphic gene expression as a biomarker (Colombo et al. 2007c; Divers et al. 2009; Amberg et al. 2010). Sturgeons are less tolerant of hypoxia than other fishes, and heavy nutrient loading can lead to reduced oxygen levels, resulting in impaired respiratory metabolism, reduction of foraging activity and growth, or death (Secor & Gunderson 1998; Campbell & Goodman 2004; Cech & Doroshov 2004; Niklitschek & Secor 2005). The improper disposal of trash leads to deformities in the Pallid Sturgeon and Shovelnose Sturgeon because rubber bands, gaskets, and other ring-shaped objects are swam into and ultimately cause notching of the rostrum, loss of barbels, broken scutes, and deformed pectoral fins (Murphy et al. 2007b).

Industrial Use of Waterways

All life stages of Sturgeons are impacted by commercial vessel passage. Shovelnose Sturgeon larvae are highly vulnerable to stranding from commercial vessel drawdown and subsequent dewatering of littoral zones when simulated in a laboratory setting. Larvae are positively rheotactic (swim toward current) and are more likely to swim toward the shoreline as water recedes (Adams et al. 1999b). Larval Sturgeons are also susceptible to propeller-induced shear stress because internal organs are underdeveloped and integument is fragile. In laboratory experiments replicating shear stress from vessels, small Lake Sturgeon larvae (mean 11 mm TL, 0.43 inch) had higher mortality (≤86%) relative to larger larvae (≤58%) (mean 14 mm TL, 0.55 inch) (Killgore et al. 2001). Juvenile and adult Shovelnose Sturgeons can be entrained by towboat propellers and have a high probability of being struck by a propeller due to their large size. An estimated 0.5 Shovelnose Sturgeons / km (0.8/mile) of towboat travel are entrained and killed in the Mississippi River navigation pool. The threat of entrainment is increased in narrow, shallow, and sluggish reaches of rivers, and higher propeller speeds increase the risk of a propeller strike (Gutreuter et al. 2003; Killgore et al. 2011). Unlike many large-river fishes, Shovelnose Sturgeons are concentrated within the navigation channel on the Mississippi River regardless of flow, temperature, or towboat traffic disturbance, putting them at high risk for entrainment mortality (Gutreuter et al. 2006, 2010).

Juvenile Sturgeons are also susceptible to entrainment during channel dredging and water diversions. Laboratory experiments show that dredge entrainment of juvenile White Sturgeons (80–100 mm TL, 3.2–3.9 inches), Pallid Sturgeons (122–168 mm FL, 4.8–6.6 inches), and Lake Sturgeons (120–173 mm FL, 4.7–6.8 inches) is likely within a radius of 1.25 m (4.1 feet) of the cutterhead of hydraulic dredges used to maintain navigation channels. Escape speeds differed between populations and sizes. Pallid Sturgeons from the Yellowstone River, North Dakota (versus Atchafalaya River, Louisiana), Lake Sturgeons from Lake Winnebago, Wisconsin (versus Wisconsin River), and smaller Sturgeons in all species demonstrated weaker swimming and thus were more susceptible to entrainment (Boysen & Hoover 2009; Hoover et al. 2011a). Water diversions in the lower Mississippi River to control flooding and restore wetlands entrain Pallid Sturgeons and Shovelnose Sturgeons into non-riverine habitat (Hoover et al. 2011b). Monitored diversions exporting water from the Sacramento–San Joaquin River, California, took on average an estimated 1,621 juvenile Green Sturgeons / year before 1986, which has decreased to an average of 79 juveniles/year from 1986 forward due to decreased abundance (Adams et al. 2007).

Disposal of dredged sediments during navigation channel maintenance can have negative impacts on Sturgeon habitat. A significant reduction in Atlantic Sturgeon relative abundance occurred in and downstream of an area where dredged sediment was disposed in the St. Lawrence River estuary, sand dunes created by dredge disposal had lower densities and biomass of prey items for juvenile and subadult Atlantic Sturgeons relative to unaffected areas, and modeling for sediment transport over 10 years predicted sediments will impact the core area used by early juvenile Atlantic Sturgeons (Hatin et al. 2007a; Nellis et al. 2007ab).

Invasive Species

Invasive species negatively affect early life stages of Sturgeons. The introduced Common Carp (*Cyprinus carpio*) feeds on the eggs of the White Sturgeon in the Columbia River (Miller & Beckman 1996), and the exotic Round Goby (*Neogobius melanostomus*) preys on eggs and perhaps larvae of the Lake Sturgeon in tributaries of the Great Lakes (Nichols et al. 2003). Invasive Zebra Mussels (*Dreissena polymorpha*) can densely colonize and essentially coat the sandy and silty habitats used for foraging by juvenile Lake Sturgeons. In habitat-choice experiments, Lake Sturgeon juveniles avoided areas with Zebra Mussels and showed reduced foraging, which may be detrimental to growth (McCabe et al. 2006). The invasive Overbite Clam (*Potamocorbula amurensis*), a known bioaccumulator of selenium, has replaced native food items of Green Sturgeons in the Sacramento–San Joaquin River, California (Adams et al. 2007). Programs to control the introduced Sea Lamprey (*Petromyzon marinus*) in the Great Lakes indirectly affect Lake Sturgeons by restricting upstream movement to spawning grounds with low-head barriers and killing of Sturgeon early life stages with lampricides (Auer 2004; Léonard et al. 2004).

Global Climate Change

Sturgeon populations will be negatively affected by the predicted impacts of global climate change on river ecosystems worldwide. Reduced precipitation and flow, increased temperature and frequency of droughts, and more extreme floods will likely exacerbate many of the existing threats to Sturgeons and their habitats. Given that many species and populations of Sturgeons are already near the upper limit of temperature for proper development and growth, they may face extinction and extirpation as global temperatures increase (Brander 2007; Ficke et al. 2007; Kingsford 2011).

COMMERCIAL IMPORTANCE

Before Europeans settled in North America, Native Americans used the flesh, roe, and oil of Sturgeons as a food source. Sturgeon skins were used to store the preserved flesh, and glue was made from a gelatin prepared from the swim bladder (isinglass) that later was used by European settlers as a clarifying agent for beer and wine. Sturgeons were a major fisheries resource for Native Americans living along the Atlantic Coast, in the Great Lakes, and in the Pacific Northwest (Ferguson & Duckworth 1997; Holzkamm & Waisberg 2004).

The caviar trade has a long history in North America. Although prized by royalty in Europe and Asia, where caviar was considered a delicacy, European settlers initially found Sturgeons distasteful and considered them a pest that could destroy fishing nets and create a hazard for small boats in some New England rivers (Bogue 2000; Saffron 2002; Spear 2007). For example, in the early days of the Lake Sturgeon fishery (ca. 1850s) in Lake Erie only a portion of the fish caught were used. At the time the huge and then seemingly worthless, net-wrecking Lake Sturgeons were mostly thrown on the beach to rot, fed to hogs, or placed in large piles and burned (Trautman 1981; Becker 1983). The species was even stacked like cordwood on the dock along the Detroit River, Amherstburg, Ontario, and used to fire the boilers of steamboats traveling along the river (Scott & Crossman 1973). The flesh eventually was used to feed servants and slaves.

The first caviar business in North America in the 1840s shipped all of its products overseas. In the 1860s–1870s local markets finally developed along the Great Lakes and Atlantic Coast, and a caviar rush ensued. But overfishing and pollution led to a collapse of the industry in 1900, and it completely ceased in 1925. Maximum catch of Lake Sturgeons reached 2,770 mt (3,053 tons) in 1885. That year, Lake Erie alone yielded 2,270 mt (2,502 tons), but the catch dropped to only 91 mt (100 tons) in 1895. Likewise catch of Atlantic Sturgeons peaked in the 1880s and early 1890s with ≥3,348 mt/year (3,691 tons) (Ferguson & Duckworth 1997; Saffron 2002; Williamson 2003). During the late 1800s a large fishery also was underway on the Pacific Coast for White Sturgeons with peak catches of 2,500 mt (2,756 tons) in the Columbia River in 1892, but unregulated overfishing led to a collapse of the fishery by the early 1900s (Williamson 2003; Van Eenennaam et al. 2004). Even the smaller so-called Shovelnose Sturgeons (actually Alabama Sturgeons) were used near the end of the fisheries with 19 mt (21 tons) harvested in the Mobile Basin in Alabama alone in 1894 (Smith 1898).

Although once supplying >75% of the world's caviar, after the North American fisheries collapsed, the caviar trade shifted to the Caspian Sea region (Van Eenennaam et al. 2004). But with the fall of the Soviet Union in 1991, unrestricted harvesting of Caspian region Sturgeons drove caviar prices down and increased the demand for this delicacy. Increased demand allowed the North American market to expand with the United States becoming the largest importer of caviar in 1999 (Raymakers & Hoover 2002; Saffron 2002). Recently production of caviar has decreased worldwide from 326 to 184 mt (359 to 203 tons) from 1995 to 2000 with prices increasing from $184 to $332/kg ($83 to $151/pound) (Raymakers & Hoover 2002). If Asian caviar exports continue to decrease from unrestricted exploitation, the demand for North American Sturgeon and Paddlefish roe likely will increase both domestically and internationally (Graham & Rasmussen 1999; Saffron 2002; Léonard et al. 2004).

In addition to caviar demand, the popularity of Sturgeons for meat and as an ornamental fish is rising internationally. Worldwide exports increased from 44.7 to 178 mt (49.3 to 196.2 tons) of flesh from 1998 to 1999 with Lake Sturgeon meat exported from Canada accounting for ≥40% of the total. Demand for live specimens, including fertilized eggs and fry for aquaculture and fingerlings or juveniles for the ornamental fish industry, is also on the rise, increasing from 0.5 to 7 million individuals over the same time frame (Raymakers & Hoover 2002). White Sturgeons were first exported to Europe in 1981 to a fish farm in Italy and in 1996 made up 51% of all Sturgeon aquaculture production in western and central Europe with all White Sturgeons (450 mt, 496 tons) produced in Italy (Bronzi et al. 1999).

Commercial harvest in North America is ongoing in four species of *Acipenser* and one species of *Scaphirhynchus* (for sport harvest, see conservation section). Canada allows harvest of Atlantic and Lake Sturgeons in only a few provinces; White Sturgeons are exploited in Alaska, Washington, and Oregon; and Green Sturgeons are harvested in Alaska and allowed as bycatch in Oregon and Washington. Species of *Acipenser* are highly regulated to avoid overharvesting. Modern-day commercial harvest of Atlantic Sturgeons peaked in 1988 at 44 mt (49 tons) and has declined in recent years, the decline attributable to a decrease in licensed fishers. In contrast, the harvest of Lake Sturgeons remained consistent, averaging 227 mt/year (250 tons/year) through the 1990s (Williamson 2003). On the Pacific Coast, commercial catch of White Sturgeons remained fairly stable from 1990 to 1995, ranging from 89.2 to 155.4 mt/year (98.3 to 171.3 tons/year). Although a coastal marine fishery exists, most harvest is from the Columbia River with an average of 10,500 specimens/year taken from 1998 to 2002 (Todd 1999; Williamson 2003). Commercial harvest of Green Sturgeons was 81.2 mt (89.5 tons) in 1991 but dropped to 10.2 and 13.8 mt (11.2 and 15.2 tons) in 1994 and 1995, respectively (Todd 1999). Many consider the flesh and roe of this species of lesser quality than that of the White Sturgeon, and this reduction in harvest may reflect a reduction in effort (Williamson 2003).

Shovelnose Sturgeons are exploited commercially in eight states within the Mississippi River basin. Commercial harvest of Shovelnose Sturgeons is poorly regulated with only half of the states allowing commercial harvest reporting harvest estimates (Todd 1999). The lack of

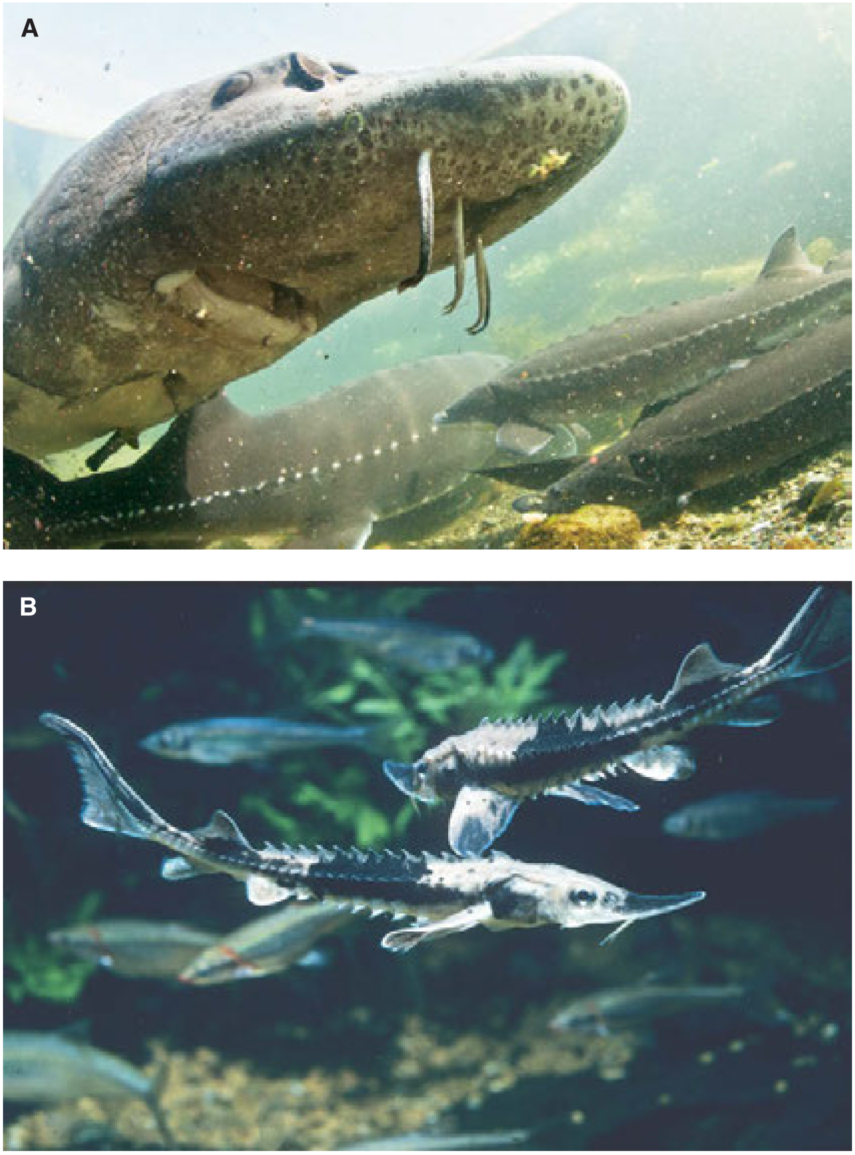

Figure 5.16. (A) Ventral view of the head of a White Sturgeons, *Acipenser transmontanus*, cruising with other White Sturgeon in a hatchery pond at the Yakama Nation Fish Hatchery, Benton County, Washington (photograph by and used with permission of Dave Herasimtschuk of Freshwaters Illustrated). (B) Hatchery-reared juvenile Lake Sturgeon, *Acipenser fulvescens*, from Wolf River, Wisconsin (photograph by B. M. Burr).

regulation stems from the perception that Shovelnose Sturgeons are common and that this species is not desirable because individuals yield low amounts of roe relative to other Sturgeons. Nonetheless harvest has increased dramatically through the 2000s. Harvest increased 51 and 87% in 2000 and 2001, respectively, in the Mississippi River in Missouri relative to the mean harvest from 1988 to 1998, and 86.5 and 5 mt (95.3 and 5.5 tons) of flesh and caviar, respectively, were taken in 2001 overall. In Iowa, harvest of Shovelnose Sturgeons more than doubled from 1997 to 2003, and the 2005 harvest was 1.6 mt (1.8 tons) valued at $158,000. Retail prices for Shovelnose Sturgeon roe climbed to $381–$1,340/kg ($173–$608/pound) in 2004 and fishing pressure is expected to increase. As such, concern is mounting for this species and there is a pressing need for regulations (Morrow et al. 1998a; Quist et al. 2002; Williamson 2003; Pikitch et al. 2005; Kennedy & Sutton 2007; Koch et al. 2009c). Between 2002–3 and 2005–6 the exploited Shovelnose Sturgeon population in the middle Mississippi River has experienced a change in sex ratio (from 1M:1F to 1.14M:1.00F), an increase in annual mortality rate (from 37% to 44%), and a decrease in recruitment through time (29%/year), a trend that will lead to a decline in population density by an order of magnitude in one decade (Tripp et al. 2009a).

With the collapse of the North American caviar industry in the late 1800s, artificial reproduction of Sturgeons was attempted with limited success in the early 1900s. Advances made in Soviet Union hatcheries over the next several decades provided the necessary information for Sturgeon facilities to begin to appear in North America in the 1960s. Aquaculture of White Sturgeons became fully established in the mid-1990s (Fig. 5.16a). Today markets exist for yolk-sac larvae for other aquaculture facilities, 2-year-old juveniles as live fish, 3- to 4-year-old subadults as food fish, and 7- to 8-year-old females for caviar and meat. In 2003, California facilities produced >6 mt (6.6 tons) of caviar with wholesale prices at $300/kg ($136/pound) and retail prices ≤$1,000/kg ($454/pound) (Van Eenennaam et al. 2004), and recent production from just 2 California farms has increased to 15 mt (16.5 tons) annually (Zhang et al. 2011). The Atlantic Sturgeon, Shortnose Sturgeon, and Lake Sturgeon are also being raised at commercial aquaculture facilities (Fig. 5.16b) (Waldman et al. 2008b).

LITERATURE GUIDE

Several sources provide excellent overviews on the Sturgeons in North America. These include edited volumes and books that cover many aspects of Sturgeon biology, management, propagation, and conservation (Willot 1991; Birstein et al. 1997c; Hochleithner & Gessner 1999; Rosenthal et al. 1999, 2002b; Van Winkle et al. 2002; LeBreton et al. 2004; Munro et al. 2007) and those that focus on harvest and conservation (Williamson et al. 1999; Williamson 2003).

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Chapter 6 Polyodontidae: Paddlefishes

Bernard R. Kuhajda

The family Polyodontidae, the Paddlefishes, has only two living species, the Chinese Paddlefish, *Psephurus gladius*, and the North American Paddlefish, *Polyodon spathula* (Fig. 6.1), although numerous fossil Paddlefishes date back to >100 mya. The Paddlefish was originally described as a Shark (Chondrichthyes, Cartilaginous Fishes) in the late 1700s due to its cartilaginous skeleton, jaw structure, and shark-like tail, but Paddlefishes are actually ancient bony fishes. Both species get large, with the North American Paddlefish reaching 2.15 m (7.1 feet) and 74 kg (163 pounds). Paddlefishes get their common names and the specific epithet *spathula* (spatula) of the North American species from the long spatula- or paddle-shaped snout that overhangs extremely small eyes and a large mouth. The Paddlefish also goes by the name spoonbill catfish in reference to the paddle and the lack of obvious scales on the body, but Paddlefishes are not closely related to Catfishes (Siluriformes). The paddle is absent in small larvae but is one-half of the body length in juveniles and one-fourth to one-third of body length in adults. The North American Paddlefish is a riverine species that feeds on zooplankton using tens of thousands of electrosensory organs covering its paddle to detect weak electric fields emitted by its prey. Zooplankton is captured by filter feeding in adults; Paddlefish pass large volumes of water into their huge mouths and filter it across extremely numerous long gill rakers, capturing the zooplankton. The name of the family and genus is derived from "poly-" (many) and "-don" (tooth), referring to the many gill rakers. The spawning habitat for the Paddlefish was unknown for >100 years until the spring of 1960 when spawning was observed on a flooded gravel bar after a rapid river rise of 2.7 m (9 feet). Upstream spawning migrations can cover >322 km (200 miles). Paddlefish populations are far below historical levels due to commercial harvest and large-river alterations (dams and channelization) that block migratory routes and destroy habitat. Paddlefish eggs are processed into caviar and are used as a substitute for Sturgeon (Acipenseridae) caviar.

DIVERSITY AND DISTRIBUTION

The Polyodontidae are restricted to the Northern Hemisphere and consist of only two extant species. The Chinese

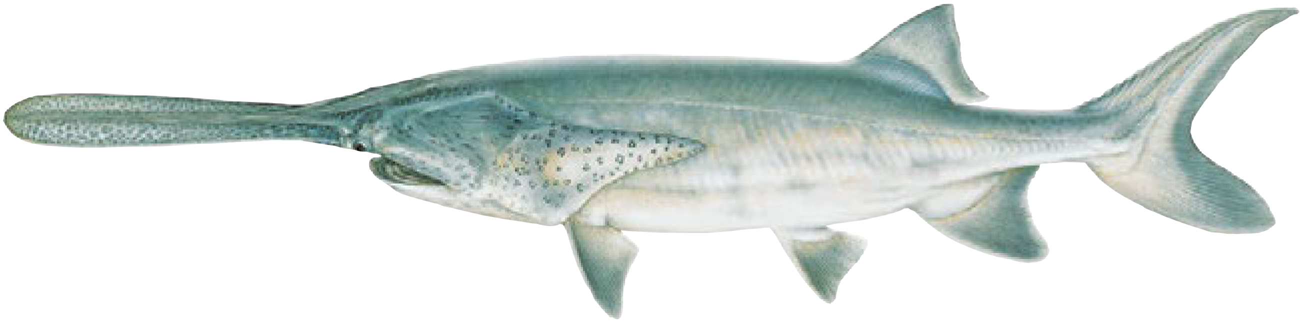

Plate 6.1. Paddlefish, *Polyodon spathula*

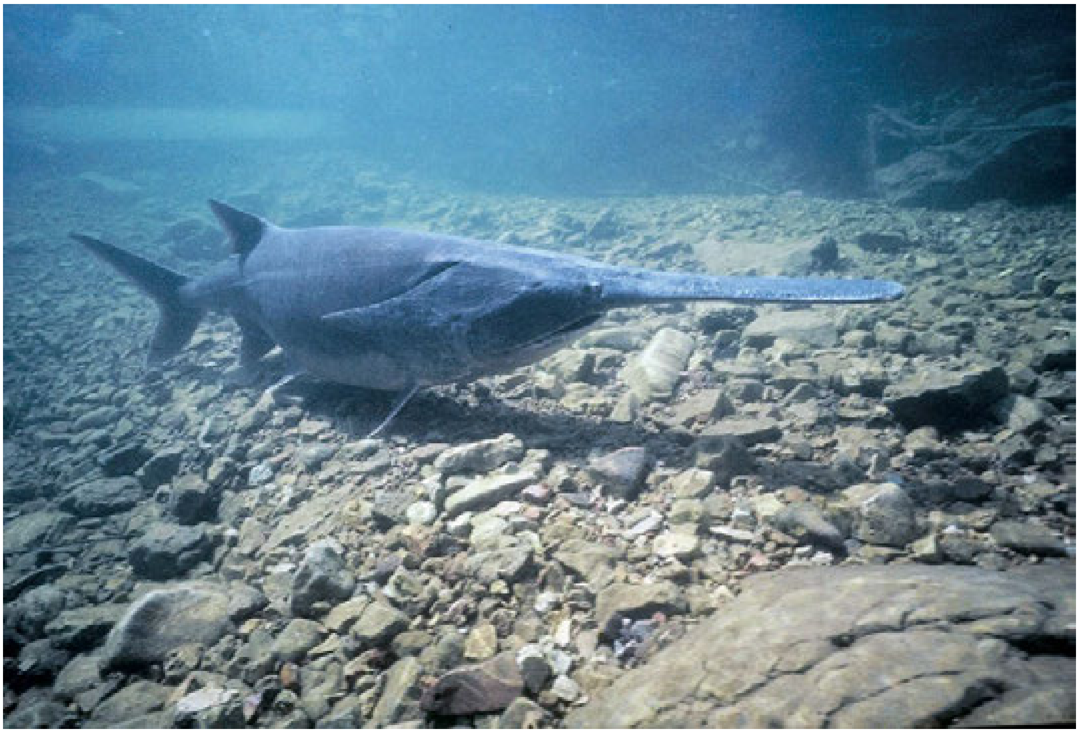

Figure 6.1. The unique Paddlefish, *Polyodon spathula*, the largest planktivorous fish in North American fresh waters, cruises in the Osage River, Missouri, one of few known spawning streams for the species (photograph by and used with permission of W. N. Roston).

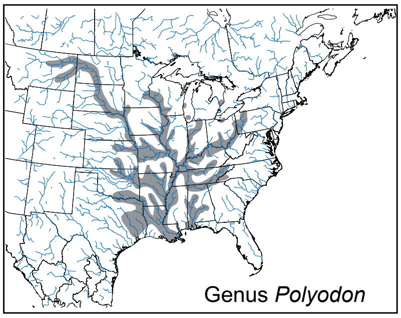

Figure 6.2. Geographic range of the Paddlefish, *Polyodon spathula*, the only extant representative of the Polyodontidae in North America.

Paddlefish (*Psephurus gladius*) occurs in the Yangtze River drainage, China, with adults occasionally migrating into the East China and Yellow Seas (Liu & Zeng 1988). The Paddlefish (*Polyodon spathula*) is a freshwater species that historically occurred in the Mississippi River basin of North America from New York to Montana and south to Louisiana and in adjacent Gulf Coast drainages from the Mobile Basin, Alabama, to Galveston Bay, Texas, as well as the Great Lakes in the United States and Canada (Table 6.1; Fig. 6.2). Although still present in most of its historical distribution in 22 states, the Paddlefish has disappeared from part of its peripheral range within the Mississippi River basin, from several western Gulf Coast drainages, and throughout the Great Lakes (Hubbs & Lagler 1964; Burr 1980; Gengerke 1986; Parker 1988; Page & Burr 1991; K. Graham 1997; Reid et al. 2007).

Inter- and Intraspecific Variation

Other than a footnote alluding to an undescribed species of Polyodontidae in the Mississippi River basin (Myers 1949), no other species of Paddlefish or any subspecies of *Polyodon spathula* are known from North America. Lower Mississippi River Paddlefish reportedly attain a greater size than those from the Ohio and upper Mississippi Rivers (Stockard 1907), but the largest and heaviest specimens recorded are from the upper Mississippi and Ohio Rivers (Nichols 1916; Forbes & Richardson 1920). Variation occurs in riverine versus oxbow lake adults from the lower Mississippi River with riverine Paddlefish possessing more slender bodies and shorter and broader paddles (Fig. 6.3) (Stockard 1907). Morphological variation in juvenile Paddlefish (61.9–403.7 mm TL, 2.4–15.9 inches) exists between populations in the southeastern United States. Hatchery-reared Paddlefish from the Mermentau River, Louisiana, possess shorter, narrower leaf-shaped paddles and asymmetrical caudal-fin lobes; hatchery-reared specimens from the Tombigbee River, Alabama, have longer, broader spoon-shaped paddles and more symmetrical caudal lobes; and field-collected juveniles from the Mississippi River, Mississippi, have the longest and broadest (paddle-shaped) paddles and symmetrical caudal lobes. Overall larger basins with higher gradients and discharges have juvenile Paddlefish with longer and broader paddles and

Table 6.1. Life history traits of the Paddlefish, *Polyodon spathula* (Polyodontidae)(—, not applicable).

Trait	Description	References
Number of extant North American species	One	Burr 1980
Strictly freshwater	Yes, few records from estuaries	Gunter 1942; Vladykov & Greeley 1963; Graham 1997; Paukert & Fisher 2000; Wojtenek et al. 2001
Maximum size recorded in length and weight	2.15 m (7.1 feet); 74 kg (163 pounds)	Nichols 1916; Forbes & Richardson 1920; Hochleithner & Gessner 1999
Maximum age	56 years	Scarnecchia et al. 2007
Age at first reproduction	Males, 5–12 years; females, 6–19 years	Lein & DeVries 1998; Scarnecchia et al. 1996b, 2007, 2011
Iteroparous or semelparous	Iteroparous	Russell 1986
Fecundity estimates (ovarian counts)	82,397–>1,000,000	Needham 1965; Robinson 1966; Russell 1986
Mature egg diameter	2.0–3.2 mm (0.08–0.13 inch)	Larimore 1950; Reed et al. 1992; Scholten & Bettoli 2005
Egg deposition sites	Over gravel, gravel and sand, and bedrock substrates	O'Keefe et al. 2007
Clutch size	No nests	Larimore 1950; Reed et al. 1992; Scholten & Bettoli 2005
Range of spawning dates and temperatures	Early March to mid-June; peak spawning occurs from 12 to 20°C (53.6 to 68°F)	Wallus 1986a; Hoxmeier & DeVries 1997; Firehammer et al. 2006
Habitat of spawning sites; average water depth	In 1.2–7.7 m of water (3.9–25.3 feet) in velocities ranging from 0.39 to 1.06 m/s (1.3–3.5 feet/s)	O'Keefe et al. 2007
Incubation period; larval type at hatching	6.5 to 10 days, 14.0–18.8°C (57.2–65.8°F); yolk-sac larvae	Ballard & Needham 1964; Yeager & Wallus 1982; Bemis & Grande 1992
Mean size at hatching	8–9 mm (0.32–0.35 inch) TL	Ballard & Needham 1964; Yeager & Wallus 1982; Bemis & Grande 1992
Parental care	None	—
Major dietary items	Crustacean zooplankton, consisting mainly of copepods and cladocerans	Eddy & Simer 1929; Rosen & Hales 1981; Hageman et al. 1986
General year-round habitat	Riverine and reservoir habitats that typically have low current velocities and high concentrations of zooplankton	Rosen et al. 1982; Southall & Hubert 1984; Moen et al. 1992; Zigler et al. 2003
Migratory or diadromous	Potamodromous, migrating to spawn or forage wholly within freshwater river systems	Bemis & Kynard 1997
Imperilment status	Paddlefish are considered Vulnerable or of Special Concern in the southeastern United States and throughout their range and are protected by 11 states	Williams et al. 1989; Graham 1997; Warren et al. 2000; IUCN 2011; Jelks et al. 2008

symmetrical caudal-fin lobes (Hoover et al. 2009a). These geographic differences are not documented for adults, but high variation of adult paddle morphology noted in large samples may obscure the existence of any distinct paddle morphotypes (Hoover et al. 2000). Similar-sized Paddlefish also have a high degree of variation in osteological features (Grande & Bemis 1991). Genetic data indicate distinctiveness of the population in Mobile Basin and perhaps other populations (see genetics section).

Paddlefish as Non-Natives

Paddlefish were first introduced outside of the United States in 1974 into Russia and are now part of polyculture systems for meat and caviar in several European, Middle Eastern, and Asian countries (Hoover 1999; Billard & Lecointre 2001; Vedrasco et al. 2001; Lobchenko et al. 2002; Raymakers 2002; Hubenova et al. 2007; Lenhardt et al. 2011). From 1993 to 1997, >1 million live Paddlefish and

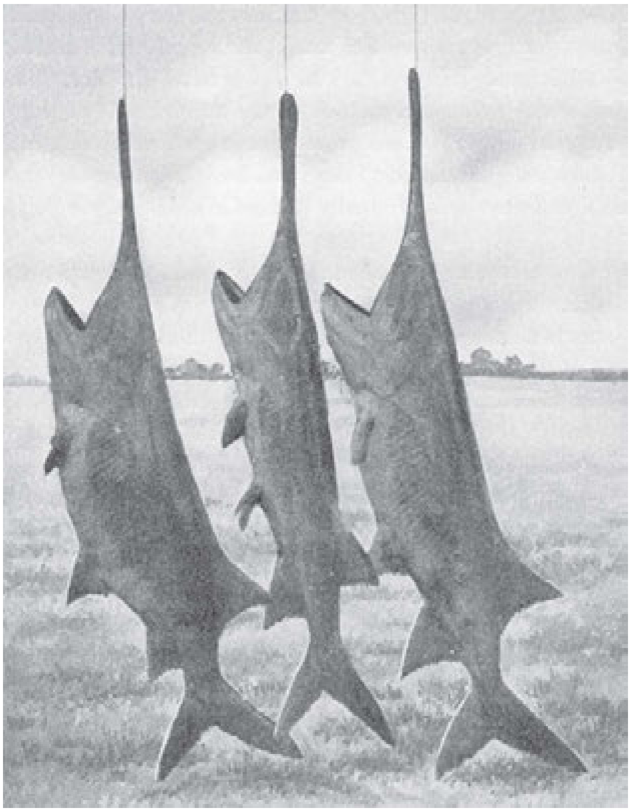

Figure 6.3. Large adult Paddlefish, *Polyodon spathula*, from the lower Mississippi River drainage demonstrating morphological variation between riverine versus oxbow lake populations, with riverine Paddlefish (middle specimen) possessing more slender bodies and shorter and broader paddles (from Stockard 1907).

fertilized eggs were exported from the United States with China importing 37% of these and establishing a culture program, raising concerns that specimens escaping into the wild could hybridize with the Chinese Paddlefish, *Psephurus gladius* (Raymakers 2002; Mims et al. 2009). Adult and juvenile Paddlefish have been captured in the lower Danube River in Serbia and Bulgaria, indicating that a population has become established, likely originating from aquaculture escapees in Bulgaria or Romania during floods (Simonović et al. 2006; Lenhardt et al. 2011). Paddlefish have also been captured in the Danube River in Austria and Slovakia (Holčik 2006). Some researchers believe a strong potential for hybridization exists between Sturgeons of the Danube River (two *Acipenser* and one *Huso* species) and introduced Paddlefish since they likely share spawning sites (Simonović et al. 2006), but others believe the threat of hybridization between these acipenserids is limited or nonexistent due to lack of appropriate habitat for the establishment of a Paddlefish population (Holčik 2006) and the demonstrated infertility between the Paddlefish and Shovelnose Sturgeon, *Scaphirhynchus platorynchus*, of North America (Mims et al. 1997, 2009; Mims & Shelton 1998).

In North America before 2001 hatcheries shared eggs and fry for stocking across the range of the Paddlefish, and Missouri River progeny were stocked in the upper Ohio and Allegheny Rivers through 2001 (Argent et al. 2009; Grady & Elkington 2009). Currently efforts are underway to ensure the genetic integrity of Paddlefish stocks are maintained by stocking with relatively local fish (Carlson et al. 1982; Epifanio et al. 1996; Heist & Mustapha 2008; Grady & Elkington 2009; Sloss et al. 2009), but some proponents of propagation and culture of Paddlefish consider genetic diversity among populations small and concern over gene-pool contamination as essentially a nonissue relative to stocking (Mims et al. 2009).

PHYLOGENETIC RELATIONSHIPS

Higher Relationships

Early researchers considered the Paddlefish (and Sturgeons) to be freshwater sharks based on their cartilaginous skeletons and jaw structures. The Paddlefish was originally described as *Squalus spathula*, the genus referring to Dogfish Sharks (Squalidae) (Walbaum 1792). Another researcher later described a new genus of shark, *Proceros*, supposedly based on a Paddlefish (Rafinesque 1820a), but the information used may have originated as a hoax (Markle 1997). The genus *Polyodon* was created when yet another Paddlefish specimen was described as *P. feuille* (Latinized to *folium*) (Lacepède 1797; McKinley 1984); the original specific name was later placed in this genus. The relationship to sharks was rejected in the mid-1800s and Paddlefishes (and Sturgeons) were considered bony fishes (Osteichthyes) and were placed in the basal grade Chondrostei (Grande & Bemis 1991, 1996; Bemis et al. 1997). Currently Paddlefishes (Polyodontidae) and Sturgeons (Acipenseridae) are placed in the suborder Acipenseroidei, and along with the fossil families †Chondrosteidae and †Peipiaosteidae, are placed in the order Acipenseriformes (Grande & Bemis 1991, 1996; Grande et al. 2002; Grande & Hilton 2006; Krieger et al. 2008; Hilton & Forey 2009; Hilton et al. 2011).

Acipenseriformes, along with Bichirs (Polypteriformes) and other fossil orders, were assigned to the subclass Chondrostei, which was basal to all other Neopterygii (Nelson 1994). But several other studies revealed that Bichirs are the extant basal actinopterygian (subclass Cladistia), and Acipenseriformes together with other fossil orders, form the subclass Chondrostei, which is sister to Neopterygii (Patterson 1982; Bemis et al. 1997; Nelson 2006).

Relationships within Polyodontidae

The first phylogenetic hypothesis for relationships between living and fossil polyodontids did not consider the fossil †*Paleopsephurus wilsoni* a member of this family but placed it as a close relative to Sturgeons (Gardiner 1984). This relationship was based largely on the erroneous reported absence of stellate bones in the paddle in the original description of the species (MacAlpin 1947) and on considering characters of *Polyodon* as primitive within the family, which was also incorrect (Grande & Bemis 1991). Current hypotheses regard the Asian fossil †*Protopsephurus liui* as the basal polyodontid, followed by the North American fossil †*Paleopsephurus wilsoni*. The living Chinese Paddlefish (*Psephurus gladius*) is basal to a monophyletic group of North American taxa, including the fossil †*Crossopholis magnicaudatus* and the genus *Polyodon* that includes the fossil †*Polyodon tuberculata* and the living Paddlefish (Fig. 6.4) (Grande & Bemis 1996; Grande et al. 2002).

Evolutionary Considerations

Fossil and recent Paddlefishes demonstrate a trans-Pacific pattern of relations dating to at least the Late Cretaceous (99.6–66.5 mya) based on minimum ages of fossils (Grande & Bemis 1991). This is corroborated with estimates of the divergence time of living Paddlefishes using molecular data that date to about 68 mya (Peng et al. 2007). Ram ventilation is used by both species of living Paddlefishes; therefore, it preceded the evolution of filter feeding in *Polyodon* (Burggren & Bemis 1992).

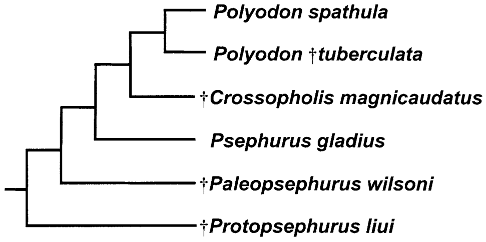

Figure 6.4. Phylogenetic hypothesis for relationships between living and fossil Polyodontidae (from Grande & Bemis 1996; Grande et al. 2002; used with permission of Lance Grande).

FOSSIL RECORD

Four species of Paddlefish fossils are currently described, three found in North America. They all possess a paddle, an extreme elongation of the snout supported by a series of long median dorsal and ventral rostral bones. They also have stellate bones present in the paddle that form a dense interlocking network and support the lateral aspects of the paddle in more advanced species. An additional polyodontid character is the presence of tiny non-interlocking scales or denticles bearing one to three anterior knobs and a posterior fringe of spines (microctenoid scales, Fig. 6.5) that cover the trunk; this character was lost in more derived Paddlefish species (Grande & Bemis 1991; Grande et al. 2002).

The fossil most closely related to the living Paddlefish is †*Polyodon tuberculata* from the Lower Paleocene Tullock Formation, Montana, dating to about 60 mya. This species is represented by only one specimen consisting of a nearly complete, but somewhat crushed, skull and part of the caudal fin. This fossil is included in the genus *Polyodon* because it shares numerous characters with *P. spathula* not found in other polyodontid fossils, including numerous long gill rakers highly modified for filter feeding, a close attachment of the upper jaw to the braincase, and an elongated and thin lower jaw. The major differences between †*P. tuberculata* and *P. spathula* may be partially developmental because †*P. tuberculata* is estimated to have reached about 2 m TL (6.6 feet), much larger than any *P. spathula* available for comparison, and Paddlefishes continue ontogenetic development their entire lifespans. Differences are basically the extent of ossification with †*P. tuberculata* possessing a heavily ossified skull with deep crests and tubercles on the dorsal surface (Fig. 6.6). Because this fossil occurs within the range of *P. spathula*, the genus *Polyodon*

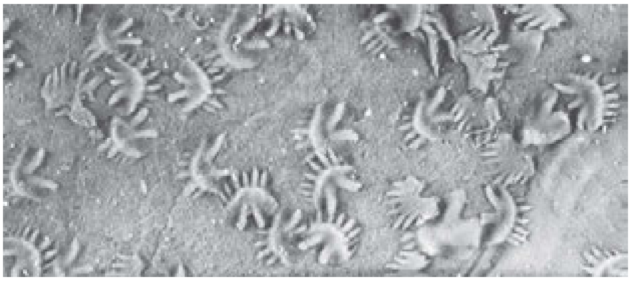

Figure 6.5. Microctenoid scales present on a specimen of the fossil polyodontid †*Protopsephurus liui*; these scales are lost in living Paddlefishes (from Grande et al. 2002; used with permission of Lance Grande).

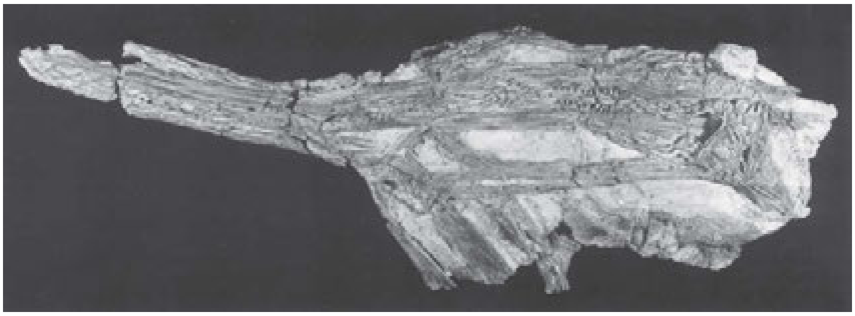

Figure 6.6. Fossil polyodontid †*Polyodon tuberculata* from the Lower Paleocene Tullock Formation, Montana, dating to about 60 mya (from Grande & Bemis 1991; used with permission of Lance Grande).

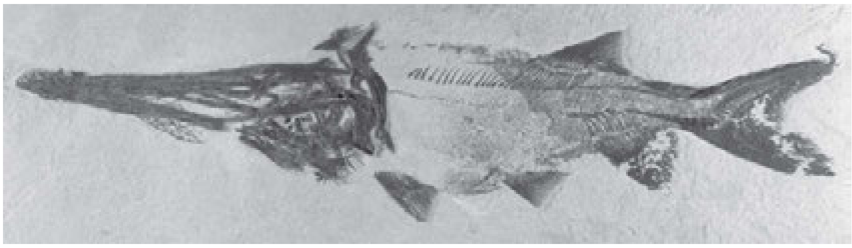

Figure 6.7. Fossil polyodontid †*Crossopholis magnicaudatus* from the Lower Eocene (50 mya) of the Green River Formation, Wyoming (from Grande & Bemis 1991; used with permission of Lance Grande).

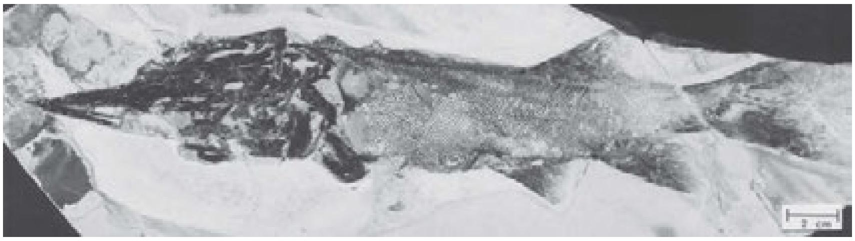

Figure 6.8. The oldest fossil polyodontid †*Protopsephurus liui*, found in formations from the Lower Cretaceous (>100 mya) in China (from Grande et al. 2002; used with permission of Lance Grande).

likely has been in the Montana area for 60 million years (Grande & Bemis 1991).

†*Crossopholis magnicaudatus* is represented by numerous specimens, some complete, from the Lower Eocene (50 mya) of the Green River Formation, Wyoming (Fig. 6.7). This fossil possesses a dense covering of microctenoid scales over most of its body not found in *Polyodon*, and its paddle tapers from a wide base to a narrow anterior end compared with the straight or anteriorly expanded paddle in *Polyodon*. Specimens range in size from 26 cm to almost 1.5 m TL (0.9–4.9 feet). Based on fossilized stomach contents, its diet was fishes, which is the same as the diet of the living Chinese Paddlefish (*Psephurus gladius*) (Grande & Bemis 1991).

†*Paleopsephurus wilsoni* is represented by a single skull, shoulder girdle, partial caudal peduncle region, and fin; these may be from 1 to 4 specimens about 56 cm TL (22 inches) that were found in Upper Cretaceous deposits (65 mya) of the Hell Creek Formation, Montana (Grande & Bemis 1991). This Paddlefish specimen, as well as three articulated Sturgeon fossils, was independently discovered in abdominal areas of hadrosaurian (duck-billed) dinosaurs (Grande & Hilton 2006; Hilton & Grande 2006). Because these fossil specimens are whole and hadrosaurs were plant eaters, the fishes likely were not eaten. Instead, the dinosaur carcasses trapped the deceased acipenseriforms and facilitated their rapid burial by forming sediment traps in near-shore or river habitats (Grande & Hilton 2006). †*Paleopsephurus wilsoni* possesses unique skull features and a stouter and more heavily ossified shoulder girdle than other North American polyodontids. As in †*Crossopholis*, †*P. wilsoni* possesses microctenoid scales on the few body parts available for examination (Grande & Bemis 1991). Past researchers did not consider †*Paleopsephurus* a Paddlefish but rather the sister-group to Sturgeons (Acipenseridae) (Gardiner 1984). This view was based partially on the reported absence of stellate bones in the paddle in the original description (MacAlpin 1947), but stellate bones were found upon additional preparation of the skull (Grande & Bemis 1991).

The oldest fossil Paddlefish by about 50 million years is †*Protopsephurus liui*, found in formations from the Lower Cretaceous (>100 mya) in China (Fig. 6.8). Although †*P. liui* possesses several polyodontid characters (e.g., elongate snout supported by a series of long median dorsal and ventral rostral bones and the presence of stellate bones and microctenoid scales), †*P. liui* lacks several derived characters found in other species and possesses a pectoral spine similar to that found in Sturgeons, indicating that this is the most basal Paddlefish. All fossil Paddlefishes, including †*P. liui*, are from freshwater deposits, indicating that their basic habitat has not changed in tens of millions of years (Grande et al. 2002).

MORPHOLOGY

Ancient Body Plan

Although the North American Paddlefish has many derived characters relative to other extant and fossil Paddlefishes, all members of this family share a basic morphology common to other acipenseriforms, including fossil taxa from the Lower Jurassic (200 mya). These relic characters include a subcylindrical body, heterocercal tail, reduced ossification of the endoskeleton and a persistent notochord, the mouth on the lower surface of the head, loss of the maxillary and premaxillary bones, fin rays more numerous than their basal skeletal supports, body scaling reduced to tiny isolated elements, and novel median V-shaped scales (fulcra) at the dorsal and ventral base of the caudal fin (Fig. 6.9). In the suborder Acipenseroidei (Paddlefishes and Sturgeons) relic characters include the endocranium greatly extended into a rostrum, dorsal fin behind the pelvic fins, pectoral fins extending laterally from a ventral insertion on the pectoral girdle, electrosensory (ampullary) organs concentrated on the underside of the rostrum, an intestine with spiral valve, a simple gas bladder with a connection to the esophagus, and no opercle with the subopercle acting as the gill cover supported by a reduced number of branchiostegal rays (one to three) (Vladykov & Greeley 1963; Grande & Bemis 1991; Bemis et al. 1997; Grande et al. 2002; Mabee & Noordsy 2004). The endoskeletal elements of the pectoral fins of Paddlefishes and Sturgeons have elements homologous to both the fin radials of teleosts and the limb bones of tetrapods (Davis et al. 2004).

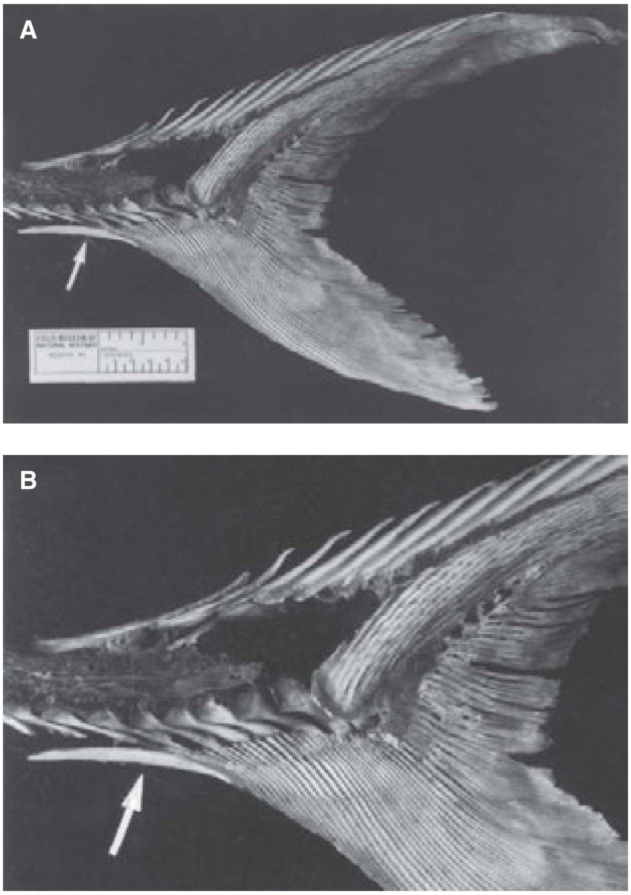

Figure 6.9. Novel median V-shaped scales (fulcra) along the dorsal edge of the caudal fin (A) and a single ventral fulcrum (B) at the caudal fin base in the caudal skeleton of a Paddlefish, *Polyodon spathula* (from Grande & Bemis 1991; used with permission of Lance Grande).

Unique Characters

All Paddlefishes are easily recognized by their extremely elongated snout (rostrum), referred to as a paddle. The paddle is supported by long medial rostral bones and an interdigitating network of lateral rostral bones called stellate bones that get their name from the star-like points radiating from their center (Fig. 6.10). Other characters unique to all Polyodontidae include a reduction in the relative size of teeth as individuals grow, the subopercle with radiating pattern of splint-like rods dorsally and posteriorly, a lateral-line canal enclosed in an ossified tube for the entire length of the caudal fin, a series of heavy dorsal caudal fulcra, a single ventral caudal fulcrum (Fig. 6.9), interlocking rhomboid scales on the upper caudal lobe, round-based scales on the shoulder and isthmus regions, and fringed (microtenoid) scales covering the trunk in fossil species (Fig. 6.5) that are replaced by vestigial denticular scales in living species. Except for the oldest and most primitive polyodontid fossil (genus †*Protopsephurus*), Paddlefishes also possess branchiostegal rays modified into a single bone with a branched posterior edge and lack a pectoral spine present in other Acipenseriformes. Living Paddlefishes have a pair of nostrils at the base of the paddle anterior and dorsal to extremely small eyes, a pair of minute barbels on the underside of the paddle anterior to

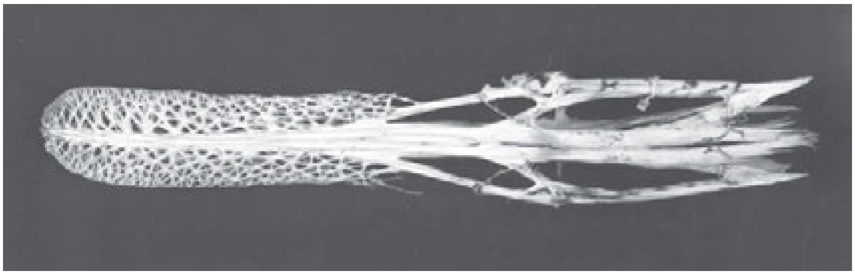

Figure 6.10. Skull of a Paddlefish, *Polyodon spathula*, with paddle supported by dorsal and ventral sheets of numerous and densely packed interdigitating stellate bones, which are attached to each other and to the median rostral bones (from Grande & Bemis 1991; used with permission of Lance Grande).

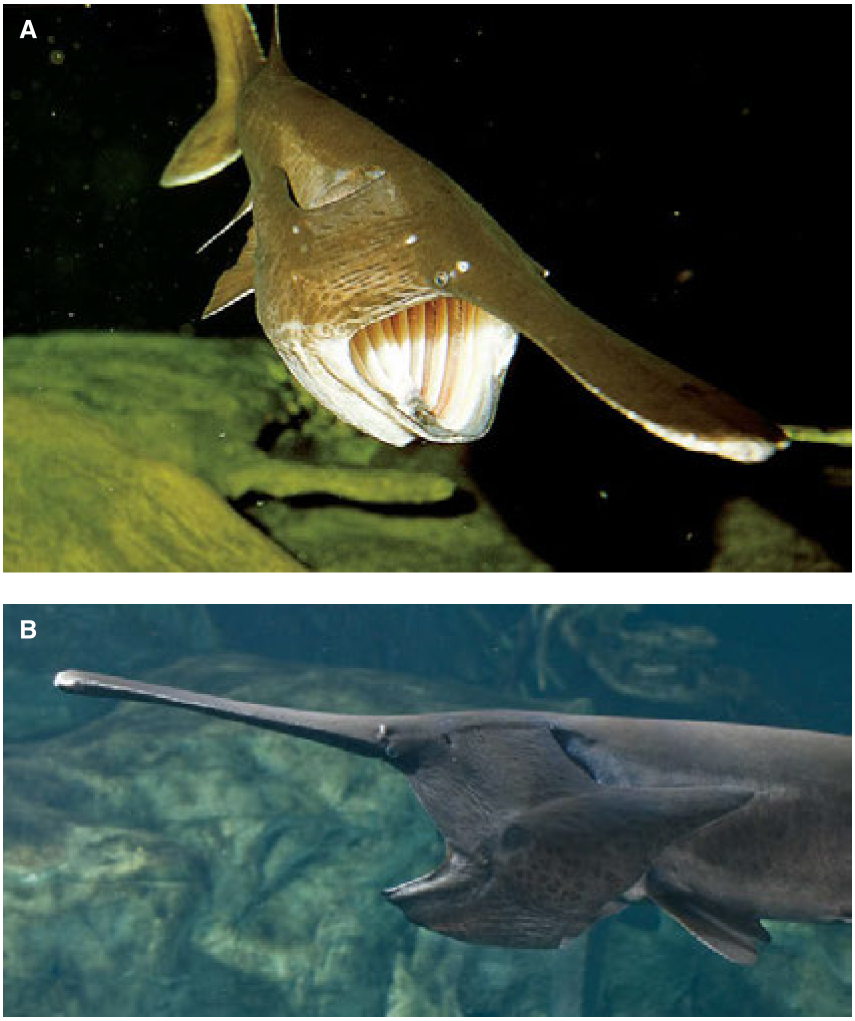

Figure 6.11. The huge gape of the Paddlefish, *Polyodon spathula*, allows a large volume of water to enter its mouth and facilitates ram ventilation and filter feeding on zooplankton (photographs by and used with permission of (A) ©Engbretson Underwater Photography, taken in Table Rock Lake, Branson, Missouri, October 2005, and (B) Todd Stailey, Tennessee Aquarium).

the mouth, a small spiracle, a fleshy tapering posterior expansion of the gill cover, and pyloric caeca present as a broad and branching organ (Forbes & Richardson 1920; Weisel 1975; Grande & Bemis 1991; Bemis et al. 1997; Grande et al. 2002; Hilton 2004).

Size

The Chinese Paddlefish is the largest extant species reaching 3.6 m (11.8 feet) and 300 kg (660 pounds). The North American Paddlefish reaches a maximum of 2.15 m (7.1 feet) and 74 kg (163 pounds) (Nichols 1916; Forbes & Richardson 1920; Hochleithner & Gessner 1999).

Filter Feeding and Electrosensory Organs

Unlike the Chinese or most fossil Paddlefishes that use protrusable jaws (similar to Sturgeons) to feed on a variety of prey, including fishes, the North American species is a filter feeder and possesses numerous morphological specializations that accommodate this mode of feeding. A large volume of water can enter the mouth of a Paddlefish because the upper jaw is firmly attached to the braincase by a short ligament and both jaws are elongate, giving the Paddlefish a huge gape as it drops its lower jaw (Fig. 6.11). Collection of zooplankton is accomplished by filtering water across extremely numerous long and flattened gill rakers (Fig. 6.12) found in a double series on gill arches compressed to wafer-like plates (Fig. 6.13). The paddle is supported by dorsal and ventral sheets of numerous and densely packed stellate bones that are attached to each other and the median rostral bones (Fig. 6.10) (Forbes & Richardson 1920; Grande & Bemis 1991; Bemis et al. 1997).

The Paddlefish can detect concentrations of zooplankton with electrosensory (ampullary) organs covering the relatively broad paddle. Both dorsal and ventral sides of the paddle are covered by dark pores that lead to ampullary organs that can detect weak electric fields emitted by zooplankton. Pores are partially filled with a jelly-like substance and occur in clusters (commonly 10–20/cluster) between stellate bones; ≤4 ampullae may share a single pore (Fig. 6.14). Ampullary organs also occur on the head and subopercle. Paddlefish have more ampullary organs (50,000–75,000) than any other fish (Collinge 1894; Kistler 1906; Nachtrieb 1910; Jørgensen et al. 1972; New & Bodznick 1985; Wilkens et al. 2002). One ampullary organ has sensory epithelium with ≤400 electrosensitive hair cells at the end of a short duct. The duct length (100–250 μm) is much shorter in Paddlefish and other freshwater fishes relative to the Lorenzinian ampullae of elasmobranchs, perhaps the result of differences in conductivity between fresh and salt water (Jørgensen et al. 1972; Neiman et al. 2000). Although the anterior lateral-line nerve innervates both ampullary organs and mechanoreceptive neuromasts of the cephalic lateral-line system, a clear division exists between these sensory systems in the hindbrain of Paddlefish (and Sturgeons) (New & Bodznick 1985). Paddlefish are unique among bony fishes in having three electrosensory pathways to deliver information from the hindbrain to the midbrain, where information for orienting movements and prey capture is processed (Hofmann et al. 2002; Wilkens et al. 2002; see behavior section). Because the sensory epithelium and the function of the ampullary organs of Paddlefish are similar to those of Lorenzinian ampullae found in elasmobranchs, the electrosensory system in Acipenseroidei likely is derived from a common ancestor shared with cartilaginous fishes (Jørgensen et al. 1972; New & Bodznick 1985; Northcutt 1986; Wilkens & Hofmann 2007).

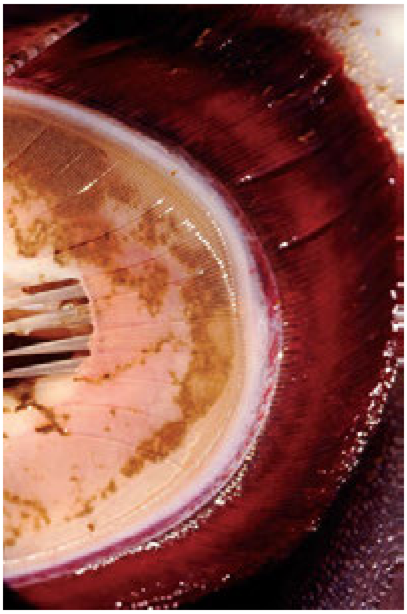

Figure 6.12. Extremely numerous long and flattened gill rakers in an adult Paddlefish, *Polyodon spathula*, allow for collection of zooplankton as water is filtered through these structures. Note the trapped zooplankton under the gill rakers (from Bemis et al. 1997; used with permission of Willy Bemis).

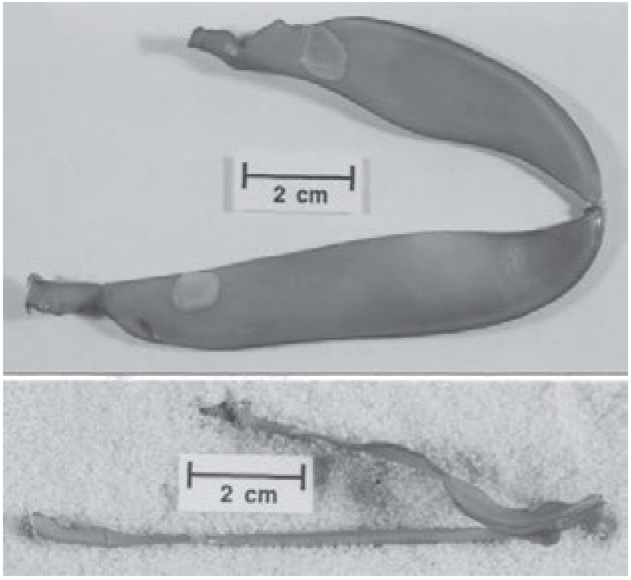

Figure 6.13. Gill arch from a Paddlefish *Polyodon spathula* laterally compressed to wafer-like plates that allows for ram ventilation. Anterior (*top*) and dorsal (*bottom*) view (from Grande & Bemis 1991; used with permission of Lance Grande).

Vision and Chemosensory System

The extraordinary development of electroreception for filter feeding is countered by a reduction of visual and chemosensory structures. Paddlefish eyes are extremely small, and the electrosensory system appears to be partially replacing the visual system in the midbrain of Paddlefish (Hofmann et al. 2002). Paddlefish have only two minute barbels anterior to the mouth on the underside of the

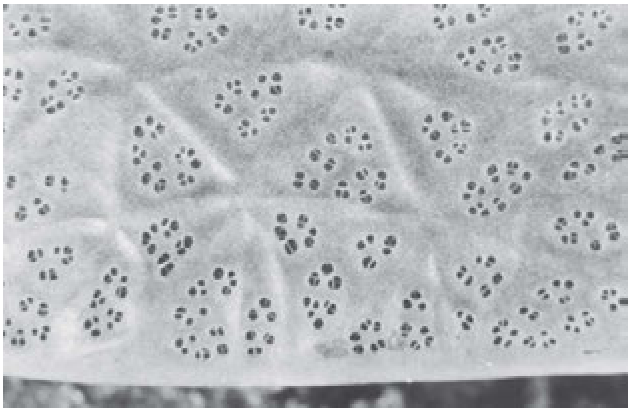

Figure 6.14. Enlarged view of dorsal surface of a Paddlefish, *Polyodon spathula*, paddle showing clusters of dark pores between stellate bones (visible through the skin of the paddle) that lead to electrosensory (ampullary) organs (from Grande & Bemis 1991; used with permission of Lance Grande).

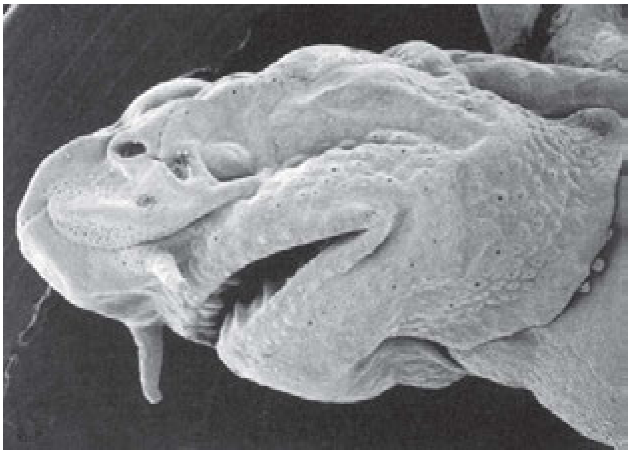

Figure 6.15. Scanning electron micrograph of larval Paddlefish, *Polyodon spathula* (stage 44), showing mouth full of small, recurved teeth that are lost in adults (from Bemis & Grande 1992; used with permission of Lance Grande).

rostrum; this contrasts with the four large barbels covered with many more chemoreceptive organs (taste buds) found in Sturgeons. Even though Paddlefish are planktivores they possess fine canine teeth that curve inward and are present in one to two rows (Fig. 6.15), but teeth are only prominent in small individuals and are shed or overgrown by bone in large specimens (Grande & Bemis 1991).

Ram Ventilation

Paddlefish lack oral and opercular valves and the jaw structure for regular pumping movements, all necessary for an effective buccal pump system for gill ventilation. Therefore they use ram ventilation, which involves steady and continuous swimming (1.25 body lengths/s for juveniles) with the mouth open slightly to allow a continuous flow of water through the oral cavity, over the gills, and out the gill cover. The long, tapering gill cover allows water to flow out of the gill chamber dorsally, caudally, or ventrally. Gill arches are held in a position that exposes the gill filaments to the direct flow of water. No other fishes as small or as slow as juvenile Paddlefish have ever been documented as ram ventilators. Ram ventilation in Paddlefish is only possible because of the extremely wide mouth gape and the lateral flattening of the gill arches. If Paddlefish are forced to stop swimming or to swim at slow speeds (<0.8 body length/s) they resort to inefficient buccal pumping for gill ventilation (Burggren & Bemis 1992). When confined to an area too small to allow swimming, Paddlefish sink to the bottom or float belly up (Bemis et al. 1997; Mims et al. 2009).

Swimming

Paddlefish are classified as cruisers, having a fusiform shape that gradually narrows posteriorly to a slim caudal peduncle with a deep, narrow caudal fin that minimizes side forces while generating substantial thrust. This allows Paddlefish to swim continuously in a straight line, which facilitates ram ventilation and filter feeding. Other structures that boost swimming efficiency include the paddle, which increases overall streamlining and reduces drag and wake, and a notch in the upper caudal lobe in juveniles (epicaudal notch; Fig. 6.16), which may minimize the downward torque of the longer upper lobe by reducing its functional length (Hoover et al. 2009a). When needed in Paddlefish, lift is most likely accomplished by changes in the vertical position of the pectoral fins, which adjusts the pitch of the paddle and provides lift, similar to how Sturgeons use their pectoral fins and rostra (Wilga & Lauder 1999; Hoover et al. 2009ab).

Other Characteristics

Other Paddlefish characters include: pale to dusky hues of bluish to olive to gray above, white to grayish sides, and whitish to milky-white below; denticular trunk scales restricted to small patches at the anterior bases of dorsal, anal, and caudal fins; a thick, compact integument to compensate for the small amount of mucus secreted; the upper lobe of forked caudal fin longer or equal in length to the lower lobe; gonads elongate and extending anteriorly along the lateral margins of the dorsal surface of the body with large masses of fat on the ventral side; and dark, spherical ripe eggs 2.0–3.2 mm in diameter (0.08–0.13 inch) (Larimore 1950; Marcoux 1966; Weisel 1975; Grande & Bemis 1991; Reed et al. 1992; Bemis et al. 1997; Ross 2001; Scholten & Bettoli 2005; Hoover et al. 2009a). The first four of five gill arches in Paddlefish have gills, and all five possess gill rakers to some extent (Rosen & Hales 1981). Paddlefish have a minute spiracle, a vestigial gill opening with a canal that leads to the gill chamber. The lower edge of the spiracle has a small barbel-like lappet. A small gill (pseudobranch) is often associated with the spiracle but is not used in ventilation (Forbes & Richardson 1920; Burggren & Bemis 1992).

Acousticolateralis System

The lateral-line system in Paddlefish is composed of a main canal on each side that runs from the tip of the dorsal lobe of the caudal fin to the dorsal side of the head, where the canal branches behind and above the eye. One branch, the supraorbital canal, leads over the eye and to the anterior nostril. The other branch, the suborbital canal, runs ventrally to below and behind the eye, continuing forward under the eye and onto the ventral side of the paddle to its tip, where it joins the canal from the other side. The hyomandibular canal is an offshoot of this branch that runs down to and behind the angle of the mouth and continues forward on the lower jaw as the mandibular canal. A supraoccipital canal is also present that does not join with the other side. This system is visible externally except for areas where it runs within or under bones, including an area directly anterior to the eye, the post-temporal area, and the paddle (Nachtrieb 1912; Grande & Bemis 1991).

Early Life Stages

Ontogenetic variation in early life stages of Paddlefish is remarkable (Fig. 6.17). Upon hatching (5–12 days post-fertilization at 11.1–18.8°C, 52.0–65.8°F, 8–9 mm TL, 0.22–0.35 inch) larvae have pigmented yolk sacs, show practically no other pigmentation, and lack any obvious Paddlefish features. As the yolk sac is absorbed organ systems develop and a pair of barbels appears anterior to the mouth. When Paddlefish begin active feeding (days 16–26, 15–17 mm TL, 0.59–0.67 inch) the yolk sac is completely absorbed, most organ systems are developed, including ampullary organs on the gill covers and head, and a blunt snout overhangs a mouth full of small, recurved teeth (Fig. 6.15) (Ballard & Needham 1964; Yeager & Wallus 1982; Graham et al. 1986; Bemis & Grande 1992). Paddlefish continue to develop as feeding larvae with differentiation of median fins, and the rostrum begins its rapid outgrowth 10 days after feeding starts. Midlateral blotches along the flanks appear at 24 mm TL (0.9 inch). Some researchers consider metamorphosis from larva to juvenile complete once median fins achieve an external appearance closely resembling that of adult Paddlefish (19 days after initiation of exogenous feeding, 36 mm TL, 1.4 inches) (Bemis & Grande 1992, 1999), others when the pectoral fin endoskeleton attains adult morphology (52 days after feeding begins, 45 mm TL, 1.8 inches) (Davis et al. 2004), and some do not consider the juvenile stage attained until all fin rays are developed (145–160 mm TL, 5.7–6.3 inches) (Yeager & Wallus 1990). During rostral growth the eyes, nasal pouches, and barbels alter their position relative to the brain, resulting in a transposition in the cranial nerves from larvae to older juveniles (Larimore 1949).

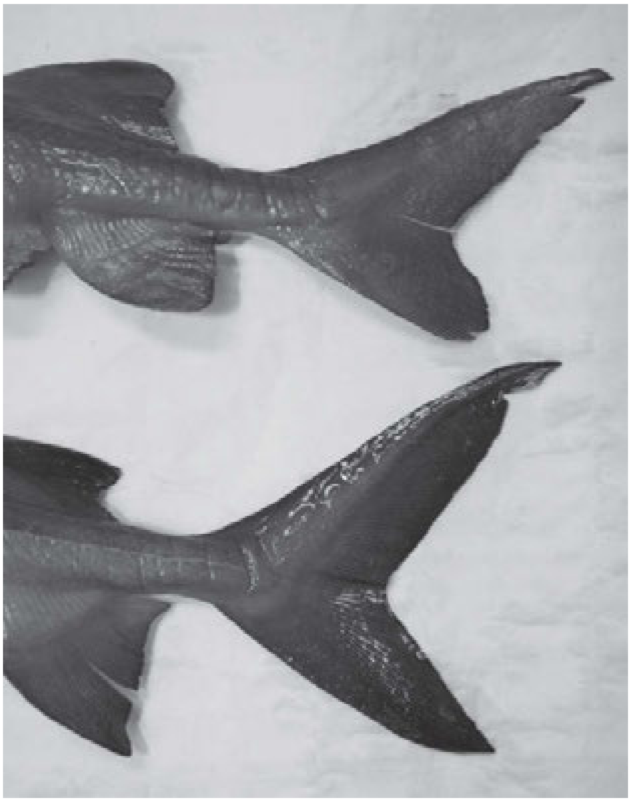

Figure 6.16. A notch in the upper caudal lobe in juvenile Paddlefish, *Polyodon spathula* (epicaudal notch), which may minimize the downward torque of the longer upper lobe by reducing its functional length (from Hoover et al. 2009a; used with permission of Jan Hoover, U.S. Army Corps of Engineers).

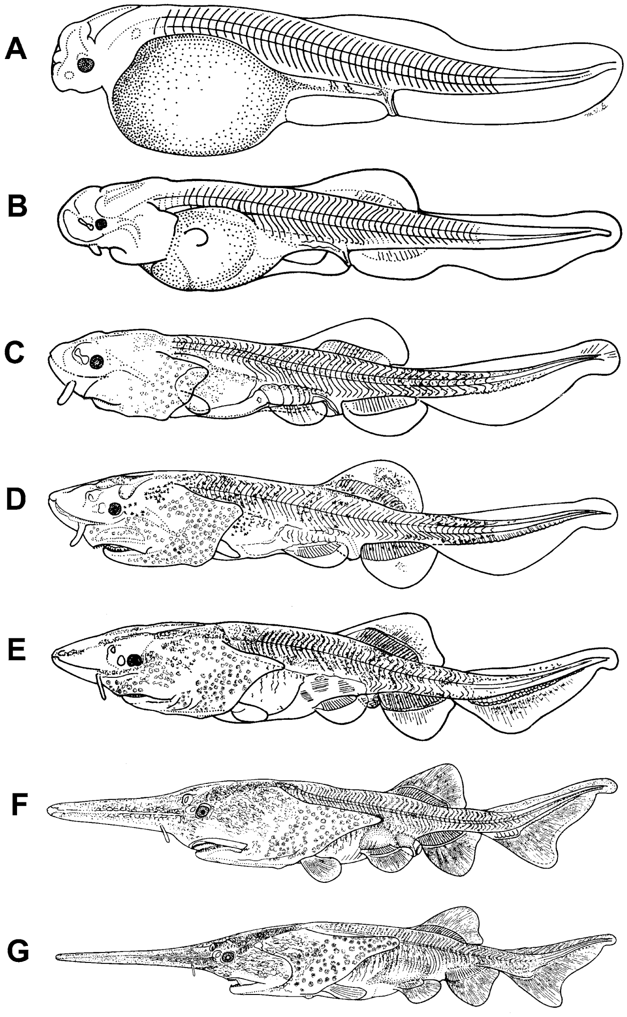

Figure 6.17. Ontogenetic changes of early life stages of the Paddlefish, *Polyodon spathula*. Newly hatched yolk-sac larvae (A) 8.9 mm TL (0.35 inch) and (B) 13 mm TL (0.51 inch). Post yolk-sac larvae (C) 17 mm TL (0.67 inch), (D) 21 mm TL (0.83 inch), (E) 34 mm TL (1.34 inches), (F) 54 mm TL (2.13 inches), and (G) 89 mm TL (3.50 inches) (from Yeager & Wallus 1990, courtesy of the Tennessee Valley Authority)

Feeding modes switch from particulate feeding in larval and small juvenile Paddlefish to filter feeding in older juveniles and adults due to ontogenetic development of gill rakers. Gill rakers do not appear on Paddlefish until they are 70–100 mm TL (2.8–3.9 inches) and are not functional as a filtering apparatus until they reach 120–170 mm TL (4.7–6.7 inches), therefore particulate feeding is accomplished through electroreception detection. Filter feeding begins when gill rakers are about 2 mm long (0.08 inch) and gill-raker spaces are slightly <0.1 mm (0.004 inch). Filter-feeding efficiency increases as the Paddlefish and its gill rakers grow (Rosen & Hales 1981; Michaletz et al. 1982; see also behavior and ecology sections).

Chemoreception does not play an important role in obtaining food during any Paddlefish life stage. Although many large oral taste buds develop in yolk-sac larvae throughout the mouth cavity and on the gill arches, they do not develop on barbels until exogenous feeding begins, and then only on the basal portion. Although the ability to detect food odor begins with exogenous feeding, few olfactory receptors are present in the nostrils of young Paddlefish; therefore Paddlefish only possess the ability to taste once food is in the mouth. Experimental studies confirm that juvenile Paddlefish have low sensitivity to food odor and must rely on passive ampullary electroreceptors for prey detection (Devitsina & Kazhlaev 1993; Kasumyan 2007; see behavior and ecology sections).

Ontogenetic changes continue through the life of the Paddlefish. Allometric growth of paddle versus body length begins with rapid paddle growth in length and width, with relative paddle length greatest (to >50% of TL) in juveniles 240–310 mm TL (9.4–12.2 inches). Growth of both anterior and posterior portions of the paddle contributes to the overall length increase. This is followed by equal growth rates, and after age 1 by greater body growth, such that paddle length can drop to <25% of TL in large adults. Paddle breadth and anterior expansion also show negative allometry in adults (Stockard 1907; Thompson 1934; Grande & Bemis 1991; Hoover et al. 2000, 2009a). Small juvenile Paddlefish (<85 mm EFL, eye-to-fork length, 3.3 inches) have longer upper caudal fin lobes relative to lower lobes. Large juveniles and adults have more symmetrical caudal lobes. A notch in the upper caudal lobe (epicaudal notch; Fig. 6.16) is present in most juveniles <400 mm TL (15.7 inches) but is lost in adults (Hoover et al. 2009a). Limited ossification of the neurocranium begins after maturation. Because large specimens are lacking for study, additional late-life ontogeny may be awaiting discovery (Grande & Bemis 1991).

Paedomorphosis

The occurrence of ontogenetic changes throughout the life of Paddlefish, specifically delayed ossification of skeletal elements, is one of the rare documented cases of paedomorphosis, defined as juvenile characters expressed in adults. Mature Paddlefish lack many skeletal ossifications present in other adult actinopterygians (Grande & Bemis 1991). Paedomorphosis may play a role in the evolution of Paddlefishes and in all acipenseriforms (Bemis et al. 1997).

GENETICS

Karyology

Paddlefish possess a karyotype with 120 chromosomes, consisting of 72 small microchromosomes and 48 larger metacentric, submetacentric, and acrocentric macrochromosomes. The existing hypothesis is that a diploid ancestor to all Acipenseriformes had 60 chromosomes, and a gene duplication event created a tetraploid (4n) ancestor (Dingerkus & Howell 1976; Birstein et al. 1997b; Ludwig et al. 2001). Some researchers consider extant Paddlefish as tetraploid, but others treat all Acipenseriformes with 120 chromosomes as functional diploids (Birstein et al. 1997b; Ludwig et al. 2001; Fontana 2002).

Low Genetic Divergence

Little genetic variation is present within Paddlefish relative to other freshwater fishes (Carlson et al. 1982; Epifanio et al. 1996). A unique aspect of all Acipenseriformes is the overall low genetic diversity at commonly used molecular markers (Birstein et al. 1997b). One hypothesis for low genetic differentiation is recent speciation of extant species in the Late Tertiary (2.5–23 mya) or possibly as late as the Pleistocene (0.01–2.5 mya) (Choudhury & Dick 1998). But most research points to an extremely slow rate of molecular evolution for all Paddlefishes and Sturgeons as the factor producing a lack of variation in genetic markers, possibly stemming from long generation times, low metabolic rates, and slow rates of concerted evolution (Krieger et al. 2000; Krieger & Fuerst 2002b; Robles et al. 2004). In general, less variation (information) is present in sequence data from the mitochondrial genome relative to nuclear loci (Wirgin et al. 1997; Robinson & Ferguson 2004).

INTRASPECIFIC GENETIC VARIATION

Allozyme and mitochondrial DNA data show the Mobile Basin population is unique relative to the Mississippi River basin and Pearl River drainage populations, and more subtle stock differences are present among major tributaries within the Mississippi River basin (Carlson et al. 1982; Epifanio et al. 1996). Nevertheless, more mitochondrial DNA studies are needed using additional genes, more sampling locations, and larger sample sizes to properly assess Paddlefish haplotype diversity (Heist & Mustapha 2008; Sloss et al. 2009). Microsatellite data support the distinctiveness of the Mobile Basin population as well the Mermentau River population, Louisiana (Heist & Mustapha 2008).

PHYSIOLOGY

Temperature Capacity

Paddlefish occur over areas with an annual temperature variation of 30°C (54°F), but they prefer and perform optimally at temperatures <25°C (77°F) (Cech & Doroshov 2004). An incubation temperature of 18°C (64.4°F) for embryos is considered optimal in a culture setting, providing for relatively quick hatching times (5–7 days) and reduction in fungus problems (Graham et al. 1986). The optimum temperature for survival and growth of larval and juvenile Paddlefish is near 20°C (68°F). Decreased survival and growth occurs at 16°C (60.8°F), and high mortalities of larvae occur at 24 and 28°C (75.2 and 82.4°F) (Kroll et al. 1992, 1994; Phelps et al. 2009). The optimum temperature for growth of adults is 7–20°C (44.6–68°F) (Rosen & Hales 1981), but Paddlefish occur in warmer habitats. In an Oklahoma reservoir, adult Paddlefish avoided high surface temperatures (≥32°C, 89.6°F) in the summer and selected water temperatures from 24 to 29°C (75.2 to 84.2°F) (Paukert & Fisher 2000). In oxbow lakes along the Alabama River, juvenile and adult Paddlefish occurred in waters that reach 33°C (91.4°F) (Hoxmeier & DeVries 1997). Higher temperatures in the southern range of Paddlefish put a higher metabolic demand on these populations that compresses their life history, leading to an overall shorter lifespan, including a shorter prime reproductive period (Scarnecchia et al. 2011).

Oxygen Requirements

Oxygen consumption increases significantly with swimming speed in Paddlefish. At the typical swimming speed of 1.25 body lengths/s (70–80% of maximum swimming speed) oxygen consumption is 70% of the maximum oxygen consumption. Paddlefish are oxygen regulators, adjusting ventilation rates to compensate for lower ambient oxygen levels. But Paddlefish are unusual in that when respiration rates start to decline under mild hypoxia (Po_2 <90 mm Hg) in the laboratory, juveniles transition from actively swimming to a complete loss of equilibrium, exaggerated buccal pump movement, and death with only a slight additional decrease in oxygen. Those that survive do not demonstrate any oxygen debt repayment after 1 h in oxygen-saturated conditions. These features indicate that juvenile Paddlefish are highly aerobic with limited capacity for anaerobic metabolism. Most oxygen-regulating fishes respond to hypoxia with increased gill ventilation through buccal pumping, but Paddlefish are not designed for this type of ventilation. When forced to stop swimming or to swim at slow speeds (<0.8 body length/s) Paddlefish attempt to use buccal pumping for gill ventilation, but the high levels of stress exhibited in these situations indicate that this method is inadequate to maintain sufficient gas exchange. Therefore the only way for Paddlefish to increase ventilation is through increased swimming speeds, but they are already near maximum speed when oxygen is at saturation, so there is little room for increased ventilation. This restricts juvenile Paddlefish to relatively well-oxygenated habitats. Large adult Paddlefish probably can tolerate lower oxygen levels as oxygen consumption generally decreases as body mass increases (Burggren & Bemis 1992). For example, adult Paddlefish occupied habitats with <5 mg/l dissolved oxygen during the summer in a prairie reservoir (Paukert & Fisher 2000).

Salinity Tolerance

Paddlefish do not typically enter the marine environment, and although a few early reports exist on movement between Gulf of Mexico tributaries or occurrence in estuary habitats, salinity levels between or at these sites were not reported (Gunter 1942; Vladykov & Greeley 1963; Graham 1997). Adult Paddlefish use Mobile Bay, Alabama, during the winter when salinity levels are relatively low (≤7 ppt) but move upstream into the Tensaw and Alabama Rivers as the bay transitions to a marine environment in spring and summer, and move several additional kilometers upstream in late summer as salt water from coastal tides moves inland along the bottom of the Tensaw River (Mettee et al. 2009). Adult Paddlefish also avoid areas of relatively higher salinity (>0.82 ppt) in a section of an Oklahoma reservoir (Paukert & Fisher 2000). Avoidance of higher salinities may be associated with the decrease in the ability of Paddlefish to detect the electric fields of zooplankton with an increase in conductivity of water (Wojtenek et al. 2001).

Metabolism

Because Paddlefish are ram ventilators they are obligate swimmers, becoming distressed when prevented from swimming. The typical swimming speed for juvenile Paddlefish is 1.25 body lengths/s, which is 70–80% of maximum swimming speed. Therefore considerable amounts of energy are expended during ram ventilation. Paddlefish, however, do not need to expend energy on muscles to power a buccal pumping system nor do they expend any additional energy on foraging since filter feeding coincides with ram ventilation. The normal minimum metabolic rate of Paddlefish is about twice the rate of other acipenseriform fishes (Sturgeons) (Burggren & Bemis 1992).

The overall metabolism of Paddlefishes and Sturgeons bridges the evolutionary gap between elasmobranchs and teleosts. Lipids are made soluble by bile that is a combination of a more primitive bile alcohol and a more advanced bile acid. Paddlefishes excrete ammonia across their gills, as do most teleosts, rather than excreting urea as in most elasmobranchs. Preliminary studies indicate that the capacity to detoxify various compounds may be lower in Paddlefish and Sturgeons compared with teleosts (Singer & Ballantyne 2004). Cortisol is the main stress steroid in Acipenseriformes and higher vertebrates. Paddlefish exhibit a much lower cortisol response compared with most teleosts when subjected to handling, chasing, and confinement. Additionally no significant changes are seen in levels of plasma glucose in response to stress in Paddlefish, but teleosts demonstrate elevated levels. Paddlefish are similar to teleosts in having elevated plasma lactate levels when physically disturbed. Overall Paddlefish appear to be less stressed than other fishes when handled (Barton et al. 1998). Plasma glucose is also low for resting Paddlefish, which is characteristic of animals that are constant feeders, and may be related to continuous filter feeding (Grant et al. 1970).

Digestion

Paddlefish are carnivores at all life stages, feeding primarily on zooplankton, and their short digestive tract reflects that of a primitive carnivore. A short esophagus leads to a secretory forestomach where chemical digestion is initiated. Paddlefish have unique large longitudinal rods of fat in the walls of the forestomach that may aid in movement of small food items and exclude large amounts of water. This is followed by the distal limb of the stomach (pylorus) that does not function as a gizzard in Paddlefish given the minute size of prey items. A pyloric sphincter separates the stomach from the intestinal bulge, an expanded upper intestine that has a diameter similar to that of the stomach. Attached to the intestinal bulge is a pyloric caecum; both of these structures facilitate nutrient absorption. The intestine continues as a thin limb that leads to the spiral valve, where a spiral, corkscrew folding of tissue increases the absorptive surface without increasing gut length. A short rectum leads to the anus. Primitive teleosts have active ciliated epithelial cells in the anterior gut, but Paddlefish have cilia that extend posterior into the spiral valve and may be important for moving minute food items. Lymph nodes are abundant in the mucosa of the intestinal bulge and spiral valve of Paddlefish, perhaps a mechanism evolved as a defense against parasitic infection. Some diffuse pancreas tissue is incorporated into the gut wall (Weisel 1973; Buddington & Christofferson 1985).

Even though the zooplankton fed on by Paddlefish are higher in lipid content relative to the macroinvertebrates and fishes preyed on by juvenile and adult Sturgeons, the lipid content of white muscle from Paddlefish is lower. Within Paddlefish red muscle has higher lipid content than white muscle (Decker et al. 1991; Singer & Ballantyne 2004).

Swimming Performance

Paddlefish are positively rheotactic, orienting head-first into flowing water. Based on laboratory observations of juveniles <115 mm EFL (eye-to-fork length) (4.5 inches), Paddlefish exhibit sustained swimming (≥200 min) at water velocities ≤40 cm/s (1.3 feet/s), which is used for foraging and depends on aerobic metabolism. Prolonged swimming (0.5–52 min) occurs at 30–50 cm/s (1.0–1.6 feet/s) and uses aerobic and anaerobic metabolism. Burst swimming is the highest speed attainable but can only be maintained for a short time (<0.5 min) at water velocities of 60–75 cm/s (2.0–2.5 feet/s) due to the accumulation of anaerobic metabolites. Paddlefish are free swimming in the water column in current, not using alternative means of movement or station holding seen in Sturgeon (e.g., hunkering, wedging, tail bracing) (Hoover et al. 2009b).

Photoreceptors and Visual Pigments

Paddlefish retinas are dominated by rods, which are sensitive photoreceptors responsible for vision in dim light, but they also possess a substantial number of cones (38%), which allow for acute and color vision under bright-light conditions. The packing density of both rods and cones is quite low relative to other animals that occupy dark environments, and thus Paddlefish likely cannot create a sharp image. Paddlefish rods and cones are uniquely robust but are structurally similar to those of other vertebrates. Rods have a relatively long, cylindrical outer segment containing photosensitive visual pigments that extends from a long inner segment of similar diameter. Rods are rather large in length and width, and likely aid in the discrimination of differences in light intensity that could aid in orienting behavior or in the detection of predators. Paddlefish cones are robust with a single tapering outer segment extending from a relatively globulose inner segment; other fishes typically have cones joined tightly together or have multiple outer segments (double, triple, or twin cones). A colorless oil globule is present within the inner segment of the cone (Sillman et al. 1999; Sillman & Dahlin 2004b). Some diurnal birds and turtles have oil globules in cones, but these are colored and assist with color vision. Only nocturnal vertebrates have colorless oil globules, and although the function is unknown, it is likely an adaptation for low-light conditions. No region of high cone density (horizontal visual streak) is present to aid in higher visual acuity (Sillman & Dahlin 2004b).

Rods in Paddlefish possess a single mid-wavelength-sensitive pigment (540 nm). Cones have pigments that are sensitive to long and mid-wavelengths (607, 535 nm). All visual pigments are porphyropsins (vitamin A_2 chromophore) that have longer-wavelength absorptive maxima compared with rhodopsins (vitamin A_1 chromophore). Since fresh water is redder (longer-wavelength visible light) than salt water, these pigments are perhaps an adaptation to freshwater habitats. All visual pigments are present throughout all life history stages. The multiple pigments in cones of Paddlefish likely enhance contrast detection across a broad spectrum, and they could even indicate the capability for color vision (Sillman et al. 1999).

Hearing Abilities and the Inner Ear

Most teleost fishes have the pars inferior of the inner ear composed of two fluid-filled pouches, the sacculus and the lagena, each containing an otolith. In the Paddlefish (and Sturgeons) the pars inferior consists of just one fluid-filled pouch with no division between the otoliths. The Paddlefish (and Sturgeons) have hair cells aligned in both horizontal and vertical planes within the inner ear, which provides evidence for directional hearing. The Paddlefish (and Sturgeons) are responsive to sounds ranging between 100 and 500 Hz and to the motion of water particles in a sound field rather than the sound pressure component (Lovell et al. 2005, 2006).

Tolerance of Extreme Environments

In the Mississippi Delta (Yazoo River drainage), Paddlefish may be restricted to the surface layer of the water column where oxygen levels (and zooplankton abundance) are higher; individuals are often seen breaking the surface with their paddles (billing), and in tank culture settings, billing is an indicator of stress. Prolonged restriction to this habitat could expose individuals to solar radiation that could damage the epidermis of the paddle (Hoover et al. 2000; Mims 2001); juvenile Paddlefish show signs of sunburn that lead to paddle deformities and mortality in unshaded hatchery raceways (Ramos et al. 1994).

Effects of Age and Interactions among Environmental Variables

Neither sex shows any increase in mortality or loss in condition at an advanced age. Older Paddlefish deplete gonadal fat bodies, which may be linked to shorter upstream spawning migrations. The only senescence reported is thinner males and a decline in gonad weight in females >35 years old in northern populations (Scarnecchia et al. 2007).

BEHAVIOR

Navigation

Paddlefish are potamodromous, migrating up rivers or streams to spawn (see reproduction section) or forage wholly within freshwater river systems (Bemis & Kynard 1997). The electrical antenna function of the paddle and its ampullary organs in Paddlefish may assist in geomagnetic detection to facilitate long-distance navigation (Wilkens et al. 1997, 2002; Gurgens et al. 2000; Wilkens & Hofmann 2007). This type of long-distance navigation is proposed for elasmobranchs (Kalmijn 1982), which have an electrosensory system similar to that of Paddlefish (New & Bodznick 1985; Northcutt 1986). A concern is the negative response of Paddlefish to electrical currents produced by metallic objects due to the metal-water interface that could disrupt their migration through locks and dams (Jørgensen et al. 1972; Wilkens et al. 1997, 2002; Gurgens et al. 2000).

Larval Dispersion

Upstream migration to spawning areas must be complemented by downstream movement of early life history stages to redistribute Paddlefish into proper habitats. Upon hatching yolk-sac larvae swim continuously and erratically, traveling in wide, random circles close to the surface. Once some of the yolk sac is absorbed (15–17 mm TL, 0.59–0.67 inch) they begin to swim in a straight line with sudden changes in direction (Purkett 1961; Ballard & Needham 1964; Yeager & Wallus 1982). This continuous swimming facilitates the passive drift of Paddlefish larvae downstream from spawning sites, which are only temporarily inundated, and into nursery areas in rivers or reservoirs where they grow and begin to mature (Purkett 1961; Wallus 1986a; Fredericks & Scarnecchia 1997). Drift of Paddlefish larvae in the Alabama River may extend 80 km (49.7 miles) downstream to oxbow habitats (Hoxmeier & DeVries 1997). As larvae 8–19 mm TL (0.32–0.75 inch) drift downstream through impounded rivers their horizontal distribution is widespread and can be evenly distributed vertically, but individuals are often concentrated near the surface. More larval Paddlefish are collected during night sampling, suggesting they may be more active at night, possibly to avoid predation. Collections of relatively large samples of larvae occurring only periodically suggest that they drift in contiguous groups (Wallus 1986a). Large Paddlefish larvae may prefer deeper habitat. In aquaria, larvae <25 mm TL (1 inch) tended to occur near the surface and large larvae were found deeper (Yeager & Wallus 1982). Large larvae also dominated samples collected with a bottom trawl (Ruelle & Hudson 1977).

Exploratory Movement

Most extensive movement by Paddlefish occurs during spawning migrations in the spring (Russell 1986; Zigler et al. 2003; see reproduction section). But non-spawning travel can encompass long distances, as seen in individuals tagged in the Missouri River, South Dakota and Nebraska. One Paddlefish traveled almost 2,000 km (1,243 miles) to the Mississippi River in Tennessee (Rosen et al. 1982) and another at large for 5 years passed through 5 dams and traveled 1,900 km (1,181 miles) to the Cumberland River, Kentucky (Stancill et al. 2002). Additionally juveniles can undergo extensive upstream movement in response to increased river flow in areas with no adults, indicating that long-distance upstream movement by Paddlefish is not solely related to spawning (Rosen et al. 1982; Pitman & Parks 1994). In unimpounded rivers Paddlefish can travel extensively with many moving 50 km (31 miles), and some 200 km (124 miles), within 3–8 months (Rosen et al. 1982).

Daily Movement

The typical speed of an adult Paddlefish ranges from 105 to 415 m/h (0.07–0.26 mile/h), and they typically travel 4.7–7.1 km/day (2.9–4.4 miles/day) (Russell 1986; Zigler et al. 1999). Large adults move greater distances within a day. Although rates of movement are similar between sexes, female Paddlefish have twice the linear range of males (Moen et al. 1992). Monthly averages of mean daily movement rates for juvenile Paddlefish range from 342 to 851 m/h (0.21–0.53 mile/h) (Roush et al. 2003). Overall, Paddlefish remain in relatively small areas during most of the year (Zigler et al. 2003), and most non-spawning movement is likely associated with food availability. In the spring and summer, juvenile Paddlefish move out of tailwater and river areas and into reservoirs where zooplankton is more abundant (Pitman & Parks 1994). Paddlefish move to downstream areas of reservoirs when higher zooplankton concentrations are present with adults moving in the winter (Stancill et al. 2002) and age-0 Paddlefish in the summer (Kozfkay & Scarnecchia 2002). Paddlefish also move longer distances and use shallower habitats at night where prey items are likely concentrated (Zigler et al. 1999; Paukert & Fisher 2000). Dams typically create formidable barriers, but a few Paddlefish can move past these structures. Most passage is in the downstream direction, but some upstream passage occurs (Coker 1929; Russell 1986; Moen et al. 1992; Zigler et al. 2003, 2004; Mettee et al. 2009).

Resting

In the early 1900s, Paddlefish were thought to hibernate during the winter and were considered most vulnerable to lamprey parasitism at this time (Beach 1902). But because Paddlefish are ram ventilators, they are obligate swimmers and never stop swimming (Burggren & Bemis 1992).

Electrosensory Systems and Feeding

Early researchers believed that adult Paddlefish fed by stirring up muddy river bottoms with their paddles and ingesting small organisms along with mud (Goode 1884; Jordan & Evermann 1896). Even when diet analyses revealed the dark stomach contents were zooplankton rather than mud, the paddle was still thought to be used to plow up the river bottom followed by backward swimming through the muddy water, where silt and prey were filtered by the long gill rakers (Forbes 1878). Researchers eventually determined that the paddle was a sensitive tactile organ covered with unprotected skin, and some correctly deduced it was used to detect zooplankton in the water column (Kofoid 1900; Wagner 1908), one even referring to the paddle as an antenna to find zooplankton (Coker 1923). Even so, many still considered the Paddlefish a bottom feeder. Small crustaceans were supposedly separated from mud either by some unspecified use of the paddle or by using the entire body to stir the silty bottom, followed by gulping of the agitated material and straining food with gill rakers (Stockard 1907; Forbes & Richardson 1920; Norris 1923; Gowanloch 1933). Some also believed that Paddlefish were herbivores and fed by raising their paddles out of the water, swimming into aquatic plants, and catching algae on gill rakers (Beach 1902).

When an extensive array of so-called primitive pores was discovered on the paddle and head of the Paddlefish, disagreement ensued over whether they were excretory organs that produced mucus (Nachtrieb 1910) or sense organs (Collinge 1894; Kistler 1906). These pores were eventually confirmed as sense organs associated with the lateral-line system (Allis 1920) and were thought to be sensitive to water vibrations and to assist in equilibrium. These assumed functions, along with observations on swimming behavior, led some researchers to conclude that Paddlefish fed by using the paddle in a side-to-side motion for dislodging small aquatic animals from vegetation (Norris 1923; Weed 1925; Thompson 1934). Eventually microscopic examination of tissues revealed that these pores contained ampullary organs that function as electroreceptors. This conclusion was supported by the observation that Paddlefish avoided the electrical current produced by the metal-water interface of an iron tube introduced into an aquarium, compared with no response when presented with a wooden rod (Jørgensen et al. 1972).

Elaborate behavioral experiments confirm that Paddlefish use their passive electroreceptors on the paddle as an antenna to detect low-frequency electrical signals produced by zooplankton through the plankton's own activities associated with swimming and feeding. Experiments were conducted in dark conditions with prey immobilized and any possible smell or taste of prey by Paddlefish blocked or masked. Even under these conditions Paddlefish detected zooplankton, indicating they can locate prey in turbid river environments without the use of visual, vibratory, olfactory, or gustatory senses. In the laboratory Paddlefish can detect their natural prey (the water flea *Daphnia* sp.) at distances ≤8.3 cm (3.3 inches), but most are detected <4.0 cm (1.6 inches). Peak sensitivity of Paddlefish electroreceptors (5–10 Hz) closely matches the low-frequency electrical oscillations (5–7 Hz) produced by the rhythmic beating of the legs of *Daphnia* used for creating water current for filter feeding. The great length of the paddle allows for prey detection before zooplankton drift past the mouth. This electrical antenna allows for effective capture of individual zooplankton by juveniles (microphagy) and likely guides adults toward concentrations of zooplankton as they filter feed (planktivory). Avoidance of metal objects placed in the water was again noted (Wilkens et al. 1997, 2001, 2002; Gurgens et al. 2000; Neiman et al. 2000). Electrosensory feeding was corroborated by eliciting strike responses from juvenile Paddlefish with artificial electrodes simulating the weak electric fields emitted by zooplanktonic prey (5–15 Hz) (Wojtenek et al. 2001). Detection of zooplankton at a greater range is possible when a noisy weak electric field at optimal amplitude is present (stochastic resonance or stochastic synchronization). Swarms of *Daphnia* zooplankton are a natural source of weak electrical noise; therefore their presence may actually boost the sensitivity of electroreceptors and allow a juvenile Paddlefish to detect a single zooplankter outlier at a greater distance (Russell et al. 1999; Neiman et al. 2000; Neiman & Russell 2001; Freund et al. 2002). The electroreceptive sensitivity of Paddlefish may also be enhanced because they are electrically quiet, using ram ventilation rather than opercular pumping, thereby avoiding ventilatory electrical interference (Neiman et al. 2000; Wilkens & Hofmann 2007). A proposed functional use for the long, tapering gill cover is to allow for better location of prey by triangulation between electroreceptors found there and on the long rostrum (Bemis et al. 1997). Paddlefish are the only fish species to use passive electroreception to feed on zooplankton; all others use this system to detect larger prey (Wilkens et al. 2001).

Paddlefish alter their swimming behavior when feeding. Slow and steady continuous ram ventilation is accompanied by swimming with the mouth slightly open and the paddle moving side to side. When zooplankton are detected by electroreception, swimming switches to increased speed in short and straight trajectories with the mouth open wider and the buccal cavity expanded (Fig. 6.11). This food search behavior is termed “ram suspension feeding.” A corresponding increase in the buccal flow velocities occurs with the increase in swimming speed during feeding (Sanderson et al. 1994; Wilkens et al. 2002; Kasumyan 2007). Paddlefish use their extremely numerous long and flattened gill rakers (found in a double series on gill arches) to filter zooplankton from the water. During filter feeding gill arches are moved to an angle that allows them to act as a sieve and filter all water entering the mouth. Paddlefish may be able to control the velocity of flow through gill rakers and the mesh size to maximize prey retentions by adjusting the position of the gill arches (Imms 1904; Rosen & Hales 1981). Taste buds present on the gill rakers and arches may aid in prey detection (Weisel 1973; Devitsina & Kazhlaev 1993). Even though mucus-secreting cells occur throughout the mouth, they do not appear to assist in prey capture by entanglement as small zooplankton are not consumed by Paddlefish (Rosen & Hales 1981). Paddlefish process zooplankton by creating a negative pressure in the buccal cavity by repeatedly slightly opening and closing their mouths, using water currents as a hydrodynamic tongue to transport zooplankton from the gill rakers to the esophagus (Sanderson et al. 1994).

Early life stages of Paddlefish either lack or have underdeveloped gill rakers and cannot filter feed. Thus, larvae and young juveniles <120–170 mm TL (4.7–6.7 inches) must selectively feed on large, slow-moving zooplankton one at a time using electroreception. Because larval Paddlefish must swim continuously to ram ventilate, efficient feeding is necessary to survive, and early development of extensive electrosensory ampullae is essential. A juvenile swims with its mouth slightly open, and when prey is detected by the ampullary organs in the paddle, the mouth opens wide to engulf the prey item, the juvenile often rolling on its side in the process. If the zooplankton is not in line with the swim path, prey capture involves more acrobatic turns and rolls (Michaletz et al. 1982; Wilkens et al. 1997, 2002).

Paddlefish with significant injuries can use electrosensory ampullae to feed successfully. An age-12 female Paddlefish presumed blind since hatching was captured in good condition in the Missouri River, indicating successful feeding that relied entirely on electrodetection of prey (Rosen & Hales 1982). Large Paddlefish occasionally have damaged or missing paddles, yet they are in good condition. Successful feeding may be accomplished through the use of ampullary organs on the head and jaw or by schooling with other Paddlefish (Wilkens et al. 2002).

Jumping

Paddlefish regularly leap out of the water, especially during the summer, often clearing the surface. Parasitic lampreys are often knocked off when Paddlefish land on their sides, so jumping may be for the purpose of removing lampreys. Even so, jumping occurs in populations with no apparent parasitism by lampreys and has been attributed to lack of oxygenated water without explanation of ostensible adaptive advantage (Beach 1902; Stockard 1907; Wagner 1908; Eddy & Simer 1929).

Sound Production

Other Acipenseriformes (e.g., Sturgeons) can produce sounds, likely from contracting muscles associated with the gas bladder (Bruch & Binkowski 2002; Johnston & Phillips 2003), and Paddlefish also may have this ability. As noted, Paddlefish frequently jump out of the water, and although this behavior is attributed to other factors (see the previous subsection), the sound produced may be a form of communication. As noted (see morphology section), Paddlefish have hair cells aligned in both horizontal and vertical planes within the inner ear that provides evidence for directional hearing (Lovell et al. 2005, 2006).

Territories

Because Paddlefish must continuously swim to ventilate, they are always on the move and do not establish home territories (Wojtenek et al. 2001), which is supported by tagging studies (Rosen et al. 1982). In culture settings juvenile Paddlefish form a hierarchy at high densities where small fish give way to large fish when a collision is imminent during feeding. Individuals in a dominant position have more freedom to feed and show greater growth rates (Gershanovich 1983).

Schooling

Although Paddlefish do not form schools where movements of individuals are coordinated they apparently do form loose schools. Irregular capture of large numbers of Paddlefish in lakes and reservoirs is attributed to schooling behavior (Wagner 1908; Pasch & Alexander 1986). As noted, successful feeding by Paddlefish with missing paddles may be accomplished by schooling with other Paddlefish (Wilkens et al. 2002).

REPRODUCTION

Age at Sexual Maturity

Paddlefish have late sexual maturation, which is an important life history parameter for their management (Birstein 1993; Bemis & Kynard 1997; Table 6.1), but aging techniques can be inaccurate and underestimate the actual age at sexual maturity (see ecology section). Males mature sooner than females, but a wide range of maturation ages exists among populations with southern populations typically maturing sooner than northern populations, which may reflect higher natural mortality, growth rates, and metabolic demands in southern populations (Reed et al. 1992; DeVries et al. 2009; Scarnecchia et al. 2011). Alabama populations mature as early as ages 5–6 for males and females (Lein & DeVries 1998), and Kentucky and Tennessee populations mature at ages 5–6 for males and age 8 for females with 100% of a year-class mature at ages 12 and 16 years for males and females, respectively (Hageman et al. 1986; Hoffnagle & Timmons 1989; Timmons & Hughbanks 2000). In Louisiana, 50 and 100% of Paddlefish are mature at 6 and 9 years for males and at 9 and 10 years for females, respectively (Reed et al. 1992), and Illinois Paddlefish mature at age 7 for males and at ages 9–10 for females (Adams 1942; Larimore 1950). Oklahoma populations typically mature at ages 6–7 for males and ages 8–9 for females (Scarnecchia et al. 2011). Populations in the upper Missouri River in Montana and North Dakota mature later (males, 8–12 years; females, 15–19 years) (Scarnecchia et al. 1996b, 2007).

Sexual Dimorphism

Female Paddlefish are typically longer and heavier than similar-aged males with the greatest differences in northern and northwestern populations (Rosen et al. 1982; Hageman et al. 1986; Scarnecchia et al. 2007, 2011). Other than size dimorphism, the sexes are similar in appearance except during the spawning season, when males have breeding tubercles on the head, opercular flaps, and body, and the urogenital papilla is somewhat raised. Females lack or have reduced numbers of tubercles, the urogenital papilla is flattened and soft, and the urogenital area becomes distended and reddish (Meyer & Stevenson 1962; Alexander & Peterson 1982; Mims & Shelton 1999). But these external characters are considered unreliable. For example, breeding tubercles can be common among mature females, and not all mature males are tuberculate (Hageman et al. 1986; Mims et al. 2009). Examination of the gonads is the only reliable way to distinguish between the sexes (Russell 1986).

Spawning Migrations

Paddlefish migrate upstream to spawning areas in the spring. Although spawning migrations vary among and within Paddlefish populations, overall patterns are present. Paddlefish congregate in deep pools before upstream migrations (Russell 1986); reservoir populations typically stage in the upper end of reservoirs or the lower end of rivers entering reservoirs (Purkett 1961; Paukert & Fisher 2001b; Scarnecchia et al. 2007; Miller & Scarnecchia 2008). Some reservoir populations have complex pre-spawning migrations in which large numbers of Paddlefish migrate in autumn and winter, moving up one tributary, then reversing direction back into the reservoir and up a second tributary, covering ≥110 km (68.4 miles) in 2 weeks (Hageman et al. 1986). Although juveniles may share pre-spawning habitat with adults in the winter (Pitman & Parks 1994), they do not typically participate in spawning migrations (Lein & DeVries 1998; Scholten & Bettoli 2005), and some males may remain in the reservoir during spawning migration (Paukert & Fisher 2001b). When the appropriate photoperiod (springtime) and water temperature (typically 12–20°C, 53.6–68.0°F) are present and water flows are high and sustained, Paddlefish begin their upstream spawning migrations. Spawning migrations of 200–322 km (124–200 miles) occur in reservoir populations (Russell 1986; Lein & DeVries 1998; Paukert & Fisher 2001b; Braaten et al. 2009a), and individuals can travel 43 km (26.7 miles) in a single day and 160 km (99 miles) in 17 days (Rehwinkel 1978; Russell 1986). Migration distances appear to be similar between the sexes (Miller & Scarnecchia 2008). Energetic tradeoffs may affect migratory distance with younger Paddlefish, which have larger amounts of stored fat, migrating farther upstream than older individuals (Scarnecchia et al. 2007). When upstream migration is blocked by dams some Paddlefish populations make synchronous downstream spawning migrations (Zigler et al. 2003). Males can arrive on the spawning grounds earlier than females (Lein & DeVries 1998; Stancill et al. 2002), but both sexes may arrive at the same time (Miller & Scarnecchia 2008). Non-spawning females may migrate upstream with spawning Paddlefish (Paukert & Fisher 2001b). Directional changes during spawning migration associated with changing levels of discharge and turbidity occur in the Yellowstone River, North Dakota and Montana, with downstream movements >20 km (12.4 miles) occurring with decreasing discharge and suspended sediment, resulting in the widespread distribution of Paddlefish in the lower 50 km (31.1 miles) of the river (Firehammer & Scarnecchia 2006).

Paddlefish can show spawning fidelity to a general area from year to year, especially for males and young females (Scarnecchia et al. 2007). Both sexes, but especially males, also show spawning fidelity to specific sites (Lein & DeVries 1998; Stancill et al. 2002; Mettee et al. 2009). As long as flows are sufficient to initiate spawning migration, Paddlefish demonstrate site fidelity whether discharge is higher and sustained or lower and fluctuating, and site fidelity can occur in different reaches of a river system. This indicates that site fidelity may be as important as discharge in determining sites visited by Paddlefish during spawning migrations (Stancill et al. 2002; Firehammer & Scarnecchia 2007; Braaten et al. 2009a). The mechanism underlying spawning site fidelity in Paddlefish is unknown. Site-specific cues may be imprinted on embryos or early larvae, or site fidelity may be established in adults through learned behavior and sensory recognition of sites (Firehammer & Scarnecchia 2007).

Paddlefish migrate downstream after spawning, and timing of movement can vary between sexes and populations. Both sexes can demonstrate strong downstream migrations into reservoirs after spawning (Stancill et al. 2002; Scarnecchia et al. 2007). Females may move downstream rapidly as males gradually move downstream (Miller & Scarnecchia 2008), or females can return to reservoirs immediately after spawning while males remain in the river for the entire spawning season (Lein & DeVries 1998). Post-spawning migrations back to reservoirs can cover 322 km (200 miles) in ≥32 days (Robinson 1966). Paddlefish typically leave the spawning area when water temperature is >13°C (55.4°F) in northern populations (Firehammer & Scarnecchia 2007), 15–19°C (59.0–66.2°F) in the mid-South (Pasch et al. 1980; Donabauer et al. 2009), and >18°C (64.4°F) in the Deep South (Lein & DeVries 1998). Although Paddlefish often make their post-spawning migration as water flows diminish (Miller & Scarnecchia 2008), variation in flows between years does not affect the time that Paddlefish remained in some rivers with many Paddlefish exiting during peak discharges (Firehammer & Scarnecchia 2007).

Seasonality

All Paddlefish populations spawn in the late winter, spring, or early summer with southern populations initiating spawning in early March, populations in the mid-South beginning in late March to April, and northern populations spawning into July (Hoyt 1984; Hageman et al. 1986; Wallus 1986a; Lein & DeVries 1998; Firehammer et al. 2006; O'Keefe et al. 2007; Braaten et al. 2009a; Donabauer et al. 2009; Table 6.1). Spawning can be delayed by deep cold-water releases from reservoirs or by the lack of a substantial water rise (Wallus 1986a; Braaten et al. 2009a).

Spawning Cues

Paddlefish begin to congregate in deeper areas within rivers or in the upper end of reservoirs in the spring at water temperatures of 10°C (50°F) before upstream migrations (Purkett 1961; Russell 1986; Paukert & Fisher 2001b; Scarnecchia et al. 2007; Miller & Scarnecchia 2008). Paddlefish can spawn at temperatures as low as 10°C (50°F) and as high as 23°C (73.4°F), but peak spawning occurs from 12 to 20°C (53.6 to 68.0°F). Spawning temperatures in the Mobile Basin, Alabama, are slightly higher than those for Mississippi River basin populations, but Paddlefish can spawn at high temperatures in Montana, where embryos are collected at 22°C (71.6°F) (Pasch et al. 1980; Wallus 1986a; Hoxmeier & DeVries 1997; Firehammer et al. 2006; O'Keefe et al. 2007).

Increasing photoperiod and water temperature control the timing of Paddlefish spawning, but the trigger for initiating upstream migration and spawning is increased flow (Russell 1986; Lein & DeVries 1998; Firehammer & Scarnecchia 2006). Slight increases in river discharge may initiate spawning migration (Lein & DeVries 1998), but large discharge pulses (>2.7 m, 9 feet) are necessary for most populations to initiate spawning activities (Purkett 1961; Pasch et al. 1980; O'Keefe et al. 2007; Braaten et al. 2009a). In reservoirs that have two or more tributaries most spawning adults migrate up the river with the highest discharge (Purkett 1961; Paukert & Fisher 2001b; Firehammer & Scarnecchia 2006; Miller & Scarnecchia 2008). Paddlefish can migrate to spawning grounds during high flows even if water temperatures are low (6–8°C, 42.8–46.4°F) (Paukert & Fisher 2001b). Substantial increases in water flow may initiate spawning, but sustained flows are necessary to ensure spawning and nursery areas are accessible and inundated (Hoxmeier & DeVries 1997; Phelps et al. 2009). Turbidity is associated with high discharge and may be an additional spawning cue. It also may aid in the survival of Paddlefish embryos and larvae by decreasing predation risk (Firehammer & Scarnecchia 2006; Miller & Scarnecchia 2008). Strong year-classes coincide with high, sustained water levels and poor year-classes occur when high flows are delayed and of short duration (Wallus 1986a; Hesse & Mestl 1993; Hoxmeier & DeVries 1997; Kozfkay & Scarnecchia 2002; DeVries et al. 2009). Spawning migration does not occur if all tributaries to reservoirs have low flows, and at such times females likely resorb their eggs (Purkett 1961; Russell 1986; Paukert & Fisher 2001b; Scarnecchia et al. 2007).

Spawning Modes and Location

Paddlefish likely have a spawning mode similar to that of Sturgeons, releasing large numbers of eggs over extensive areas of river bottom (i.e., broadcast spawning) (Purkett 1961; Cherr & Clark 1985; Parsley et al. 2002). Paddlefish release only a small quantity of eggs at a time, so females take 8–10 h to complete ovulation (Graham et al. 1986). Paddlefish may be fractional (intermittent) spawners (Pasch et al. 1980; Yeager & Wallus 1990), but no details are available on whether the same female is releasing eggs at intervals of days or weeks.

Spawning grounds for Paddlefish were unknown for more than a century, although early observations indicated that mature and spent females and males generally occurred over somewhat hard and sandy bottoms in Louisiana (Alexander 1915). The first recently hatched Paddlefish larvae ever discovered were 7 specimens 17–20 mm TL (0.7–0.8 inch) collected from the head of an island in the Mississippi River in Illinois in 1932 (Thompson 1933). Four more larvae 17–26 mm TL (0.7–1.0 inch) were captured in the Mississippi River in Missouri in 1944 near an island (Larimore 1949). But it was not until 1960 that spawning was first documented, occurring over an inundated gravel bar with current in the Osage River, Missouri, after a rapid water rise of 2.7 m (9 feet). Spawning was verified by the collection of embryos and newly hatched larvae 4 days later on the exposed bar after a rapid fall in water levels of 2.1 m (6.9 feet) (Purkett 1961). Additional embryos were captured using benthic samplers in streambeds with gravel and rubble at depths of 2–12 m (6.6–39.4 feet) (Pasch et al. 1980), in 0.9–4.9 m of water (3–16.1 feet) over or near gravel and rubble (Firehammer et al. 2006), and at a depth of 7.7 m (25.3 feet) over bedrock substrate in high-velocity areas (O'Keefe et al. 2007). In general spawning occurs over gravel, gravel and sand,

and bedrock substrates in 1.2–7.7 m of water (3.9–25.3 feet) in velocities ranging from 0.39 to 1.06 m/s (1.3–3.5 feet/s) (O'Keefe et al. 2007). Although Paddlefish may use tailrace habitat below dams for spawning as inferred from collections of larvae downstream of dams (Pasch et al. 1980; Wallus 1986a; Hoxmeier & DeVries 1997; Donabauer et al. 2009), no embryos have been collected in these areas using benthic samplers (O'Keefe et al. 2007).

Courtship

No evidence of courtship or pre-spawning pairing exists in Paddlefish. Observations, however, are extremely limited because of turbid spawning habitats (Purkett 1961; Scarnecchia et al. 2007).

Spawning

Details on the act of Paddlefish spawning still remain a mystery. One account by a commercial fisher from the early 1900s described a probable act of spawning as a congregation of Paddlefish at an overflow border of a bayou in April that were not frightened even when he killed nine with an oar (Stockard 1907). Another fisher described loud splashing near an island in a river during early evening with one individual, presumably the female, lying fairly quietly while others, presumably males, continually leaped about her body on all sides (Thompson 1933). The only spawning act verified by finding Paddlefish embryos and newly hatched larvae occurred on an inundated gravel bar in April 1960. A single Paddlefish appeared at the surface, agitated its caudal fin several times for a few seconds, then disappeared. This behavior was repeated every few minutes during the late afternoon and into the evening. From these limited observations, a spawning rush may have occurred starting a considerable distance under the surface in which eggs were released with the rapid agitation of the caudal region by the female and presumably the simultaneous release of milt by accompanying males. The observed surface activity likely occurred as the female surfaced at the apparent end of the rush (Purkett 1961). Paddlefish are broadcast spawners, and the above spawning scenario is consistent with other broadcast-spawning fishes, including Sturgeons, where the female spawns with several males in a series of individual spawning rushes over extended periods (Bruch & Binkowski 2002). Other spawning activities occurred after 2 and 10 days, the latter following a rapid water fall of 2.1 m (6.9 feet) and another rise of 3.4 m (11.2 feet) (Purkett 1961). Paddlefish may be intermittent spawners, but whether the same or different individuals engaged in these additional spawning events is unknown.

Parental Care

Paddlefish do not exhibit any parental care (Scarnecchia et al. 2007). This is typical for broadcast spawners (Bruch & Binkowski 2002).

Breeding System and Sex Ratios

The breeding system of Paddlefish is unknown, but most broadcast spawners, including the Lake Sturgeon, *Acipenser fulvescens*, and probably most other Sturgeon species, are polygamous (Bruch & Binkowski 2002). Although observations are limited, no competition appears to occur between male Paddlefish for exclusive breeding opportunities (Scarnecchia et al. 2007). Several males are likely involved in the spawning act with a single female (Purkett 1961), again similar to the Lake Sturgeon (Bruch & Binkowski 2002), but another broadcast spawner, the Shortnose Sturgeon (*A. brevirostrum*), may pair bond (Dadswell 1979).

Sex ratios in Paddlefish during the spawning season are near 1M:1F (Rosen et al. 1982; Hoffnagle & Timmons 1989; Hoxmeier & DeVries 1997) or slightly favor males (1.5M:1F to 2M:1F) (Robinson 1966; Rehwinkel 1978; Hageman et al. 1986; Lein & DeVries 1998). Some sex ratios are extremely skewed toward males (35.9M:1F) but are attributed to males migrating before females (Robinson 1966).

Reproductive Allocation and Spawning Frequency

Gonads of middle-aged spawning female Paddlefish are 20% of body weight compared with <1.5% for males. Given the large amount of energy necessary to develop mature eggs, most female Paddlefish do not spawn yearly, but males can spawn every year (Russell 1986; Scarnecchia et al. 2007). In the upper Missouri River, Montana and North Dakota, male Paddlefish spawn every 1–2 years and females every 2–3 years (Firehammer & Scarnecchia 2007; Scarnecchia et al. 2007). Some females, however, may spawn annually. In Alabama, individuals of both sexes participate in upstream migrations in consecutive years, including gravid females (Lein & DeVries 1998), and in Kentucky Lake, all mature females (specimens >1,034 mm EFL, 40.7 inches) collected during a study were gravid (Scholten & Bettoli 2005).

Fecundity

Fecundity as gonadal weight relative to body weight increases in young adults 15–24 years old, remains steady in middle-aged Paddlefish 25–35 years old, and decreases in older females >36 years in Montana and North Dakota (Scarnecchia et al. 2007). Relative fecundity in females is positively correlated to body weight and, in some instances, body length (Hoxmeier & DeVries 1997; Lein & DeVries 1998; Scholten & Bettoli 2005). For example, the fecundity (F) of Paddlefish females in the Alabama River is estimated as F = 31,656.6 (body weight) − 205,121 and F = 1,614.2 (body length) − 1,290,063 (Lein & DeVries 1998). Examples of fecundity as total number of eggs/female include 82,397 eggs for a small, young female (7.5 kg, 16.5 pounds), 269,043 and 371,480 eggs for larger and middle-aged females (21.2 and 18.1 kg, 46.7 and 39.9 pounds, respectively), and 608,650 and >1,000,000 eggs for large and older females (30.8 and 35.8 kg, 67.9 and 78.9 pounds, respectively) (Needham 1965; Robinson 1966; Russell 1986; Table 6.1). Higher fecundity rates may compensate for shorter lifespan in southern populations. Alabama and Tennessee populations average >19,000 and 16,381 eggs/kg body weight (>8,618 and 7,430 eggs/pound), respectively, compared with an average of 12,864 eggs/kg body weight (5,835 eggs/pound) in Montana (Hoxmeier & DeVries 1997; Lein & DeVries 1998; Scholten & Bettoli 2005). An exception is Paddlefish in Louisiana where fecundity is low (9,484 eggs/kg body weight, 4,302 eggs/pound) but is accompanied by a larger egg diameter (mean 2.67 mm, 0.11 inch, to 3.1 mm, 0.12 inch) (Reed et al. 1992).

Gametes

An acrosome is a cap over the sperm head that contains enzymes involved in sperm penetration through the egg's extracellular envelope (chorion). Most actinopterygian (Ray-finned) fishes have eggs that possess a single funnel-shaped micropyle at the animal pole that allows a single sperm to make direct contact with the egg's inner plasma membrane for fertilization, eliminating the necessity for an acrosome on sperm (Zarnescu 2005). Both Paddlefishes and Sturgeons are unique in that sperm possess an acrosome even though eggs have a micropyle, and both are unique in having eggs with numerous micropyles. Paddlefish eggs possess 4–12 micropyles and have specialized sperm entry sites in the egg surface under each micropyle (Linhart & Kudo 1997). When the acrosome is activated, a fertilization filament (acrosomal process) forms that aids in fertilization. Within vertebrates only Lampreys (Petromyzontidae), Paddlefishes, and Sturgeons possess an acrosomal process. Paddlefish sperm are elongate with a rod-shaped head, a midpiece, and a long flagellum with two lateral projections or fins (Zarnescu 2005). These gamete morphologies are potential reproductive adaptations for acipenseriforms to successfully broadcast spawn in a riverine environment (Cherr & Clark 1985).

Egg, Sperm, and Environment Interactions

Paddlefish sperm is activated upon contact with fresh water and can have motility for ≥9 min (Cosson et al. 2000; Linhart et al. 2002). Upon contact between egg and sperm cytoplasmic processes (fertilization cones) form within micropyles, blocking entry for other sperm and likely preventing polyspermy (Linhart & Kudo 1997).

Embryo Characteristics and Development

Fertilized eggs (embryos) are demersal, 2.0–3.2 mm (0.08–0.13 inch) in diameter, and adhesive immediately after fertilization, often attaching singly to a pebble or rock (Purkett 1961; Needham 1965; Yeager & Wallus 1982). Length of time to hatching is variable and dependent on temperature with faster development at higher temperatures, but Paddlefish embryos typically hatch in 6.5–10 days (Ballard & Needham 1964; Yeager & Wallus 1982; Bemis & Grande 1992).

Although 31 developmental stages are identified for Paddlefish embryos, ranging from the fertilized egg up to hatching, the numbering scheme is altered to correspond with similar stages in Sturgeons, so that hatching is considered to occur at stage 36 (Table 6.2). The major stages and events of embryonic development include fertilization, cleavage, blastula formation, gastrulation, neurulation, initiation of organogenesis, head lift, tail separation, and hatching. Paddlefish undergo holoblastic cleavage, in which each cleavage divides the entire egg cytoplasm, including the yolk. Because Paddlefish eggs are large and have significant amounts of yolk concentrated at the vegetal pole, the process of cleavage is slow except at the animal pole; thus, when the first cleave is complete, several more have already formed at the animal pole. A secretion from the hatching gland facilitates hatching of Paddlefish embryos (Ballard & Needham 1964; Bemis & Grande 1992; Bolker 2004).

Table 6.2. Embryonic stages of Paddlefish, *Polyodon spathula*, reared at 14°C (57.2°F) (from Ballard & Needham 1964). Some stages combined to correspond to embryonic stages of Sturgeons.

Stage	Time Post-Fertilization	Description of Embryo
1	<2 h	Uniform color; no activation visible; pole axis horizontal
2	<2 h	Embryo rotates 90 degrees, animal pole up with white cytoplasm surrounded by ring of dark pigment
3	<2 h	Light area appears on one side of animal pole
4	2–6 h	First cleavage furrow forms
5	2–6 h	Second cleavage furrow forms
6	2–6 h	Third cleavage furrow forms
7	7 h	Fourth cleavage, separation of macromeres from micromeres
8	8 h	Fifth cleavage forms
9	10 h	Seventh cleavage, defined as such to parallel Sturgeon stages
10	>10 h, <24 h	Late cleavage, marginal zone of cells noticeable
11	24 h	Early blastula, upper surface still pebbled in appearance
12	28 h	Late blastula, upper surface smooth
13	32 h	Blastocoel roof thinned and protrudes blister-like; gastrulation movements begin
14	35–38 h	Invagination begins as furrow at equator between gray-white epibolic cells and dark brown vegetal cells
15	38 h	Epibolic cells move below equator; dark brown yolk plug diameter > one-half of embryo
16	42 h	Yolk plug diameter half of embryo
17	44–55 h	Yolk plug diameter one-fourth of embryo; embryo rotates in membrane with future dorsal side up and yolk plug at equator
18	55–58 h	Yolk plug nearly buried; slit blastopore with dorsal-lip notch
19	65 h	Yolk plug buried; slit blastopore still present, neural groove extends short distance from slit
20–21	68 h	Neural folds prominent but not closed together
22	71 h	Neural folds meet at trunk but not at brain level; embryonic axis wraps 150 degrees around yolk
23	78 h	Neural folds completing closure at brain level; brain vesicles appear; one to three pairs of somites appear with kidney ridges lateral
24	90 h	Embryonic axis wraps 200 degrees around yolk; kidney duct bows outward from somites 4–7; optic vesicles and otic placodes appear; trunk-tail bud as broad, slight mound; head parts not raised; mandibular segments appear
25	4 days	Pronephric bends of kidney ducts extend forward
26	4.75 days	Trunk-tail bud as flat, blunt paddle slightly undercut; mandibular arches with wing-like expansions to level of optic vesicles
27–28	5.5 days	Trunk-tail bud projects flat or rod-like, not as long as brain; heart straight or slightly bent tube without chambers, beats feebly
29	6.25 days	Trunk movements present; trunk-tail bud curved, finger-like, as long as brain; head raised off yolk surface, but not undercut
30–31	6.75 days	Trunk-tail free and beginning to straighten, three-quarters length of yolk sac; head undercut to eye; median fin fold and segmentation process developed beyond cloaca
32–33	7.75 days	Length 7.5 mm; trunk-tail axis continues to straighten; fin fold narrow, reaches near tip of tail; opercular border of hyoid segment bulges prominently anterior to branchial segment
34–35	9 days	Length 8 mm; first hatching; tail nearly straight; tail fin developed for swimming; segmentation almost complete; head undercut past lower jaw; heart begins showing chamber bulges; ear vesicle outline from round to oval
36	10 days	Mass hatching; tail straight; head undercut to pericardial cavity; embryo with practically no melanophores

Larval Development

Upon hatching larvae use their yolk sac for nutrition as organ systems continue to develop, including the mouth, gut, gills, circulation, fins, and sensory structures (Ballard & Needham 1964; Bemis & Grande 1992; see morphology section).

ECOLOGY

Habitat

Outside of the spawning season adult Paddlefish use a variety of habitats that typically have low current velocities and high concentrations of zooplankton. In impounded and channelized rivers adult Paddlefish predominantly select tailwater scour holes below dams with low to moderate current, where depths average 7.0–15.7 m (23.0–51.5 feet) and current velocities are 9–32 cm/s (3.5–12.6 inches/s) (Southall & Hubert 1984; Moen et al. 1992; Zigler et al. 2003; Table 6.1). The narrow constriction of rivers at dams may funnel and concentrate zooplankton from a reservoir into tailwater releases (Coker 1929), and current patterns may allow Paddlefish to filter feed in tailwaters without substantial movement (Southall & Hubert 1984; Moen et al. 1992; Pitman & Parks 1994). Juvenile Paddlefish also strongly select tailwater and deep-water habitats (median depths 5.2–6.1 m, 17.1–20.0 feet) (Barry et al. 2007). Paddlefish also occur in deep main channel border habitats and congregate near artificial structures that provide scour holes with areas of reduced current velocities (mean depth 6.7 m, 22 feet, mean current velocity 30 cm/s, 11.8 inches/s); these structures may simulate sandbars and other natural structures present before impoundment and channel modifications (Southall & Hubert 1984; Moen et al. 1992; Pitman & Parks 1994). Paddlefish also concentrate in main channel border habitats near backwaters, presumably to use high amounts of invertebrate drift from backwaters (Southall & Hubert 1984; Moen et al. 1992). River bends and secondary channels with deep-water habitats (>6 m, 19.7 feet) and slow flows (<5 cm/s, 2 inches/s) also are used (Zigler et al. 1999, 2003). Both adult and juvenile Paddlefish use deep water during the winter (Rosen et al. 1982; Pitman & Parks 1994), which may provide valuable habitat throughout the year (Moen et al. 1992; Stancill et al. 2002). During the post-spawning period and into summer Paddlefish use shallow backwater areas that average 2.3 m (7.5 feet) deep with current velocity of only 6 cm/s (2.4 inches/s) (Southall & Hubert 1984). Deep impounded creek mouths adjacent to shallow flats are also used by post-spawn females in the summer; these habitats may function similarly to oxbow lakes in unchannelized rivers (Donabauer et al. 2009). Reservoirs are used extensively by juvenile and adult Paddlefish. They typically inhabit deep areas (>3.4 m, 11.2 feet) with little or no current (median 11.3 cm/s, 4.4 inches/s) with juveniles occupying surface waters (Fredericks & Scarnecchia 1997; Paukert & Fisher 2001a; Kozfkay & Scarnecchia 2002; Zigler et al. 2003). When both river and reservoir habitats are available to juvenile Paddlefish, they occupy tailwater and river habitats during winter and reservoirs during spring and summer (Pitman & Parks 1994).

In unimpounded and unchannelized rivers adult Paddlefish occur downstream of submerged sand bars at depths of 2–3 m (6.6–9.8 feet) with slow flow (0–30 cm/s, 0–11.8 inches/s) in the summer and occasionally use backwater areas below islands or irregular shorelines. In the winter, Paddlefish occupy areas ≥3 m deep (9.8 feet) with little flow (Rosen et al. 1982). From mid-April to mid-July in the middle Mississippi River, age-0 Paddlefish 10–170 mm TL (0.4–6.7 inches) avoid the main channel and select island habitat with moderate current (0.4–0.6 m/s, 1.3–2.0 feet/s) and depth (3–5 m, 9.8–16.4 feet) over a sand substrate. Microhabitat includes inundated terrestrial vegetation likely used as foraging habitat or as a refuge from predation (Phelps et al. 2009). Backwater areas are used by juveniles and adults primarily during summer and autumn in the lower Alabama River, when zooplankton densities are highest. Pre-spawning migrations of adults into channel habitats occur during winter and spring with juveniles in backwater habitats often accompanying adults. Oxbow lakes along the Alabama River have high primary productivity and are used exclusively by juveniles as nursery areas, where they remain until sexual maturity (Hoxmeier & DeVries 1997). Juvenile Paddlefish also use oxbow lakes along the Arkansas River, but adults are also present during summer when oxbows are disconnected from the river (Clark-Kolaks et al. 2009).

Diet

Adult Paddlefish are planktivores and feed almost exclusively on crustacean zooplankton, consisting mainly of copepods and cladocerans (Eddy & Simer 1929; Rosen & Hales 1981; Hageman et al. 1986; Smith et al. 2009b). Adult Paddlefish are nonselective plankton feeders in terms of what enters their mouths, but the gill rakers are selective relative to size with small plankton (<0.20–0.25 mm long, 0.008–0.01 inch, and 0.1–0.2 mm wide, 0.004–0.008 inch) passing through these structures. This all but eliminates small zooplankton and all phytoplankton from the diet. Large zooplankton are consumed in proportions relative to their presence in the water column (Eddy & Simer 1929; Rosen & Hales 1981; Smith et al. 2009b). Insect larvae, mainly ephemeropterans (mayflies) and chironomids (midges), are also consumed and can be a significant portion of the diet when present in the water column in preparation for emergence as adults (Wagner 1908; Coker 1923; Hoopes 1960) or when flooded vegetated bars are available for foraging (Hoxmeier & DeVries 1997). Other items consumed include algae, amphipods, ostracods, and rotifers (Forbes 1878; Eddy & Simer 1929; Rosen & Hales 1981; Blackwell et al. 1995; Hoxmeier & DeVries 1997). Fishes, typically shad (*Dorosoma* spp.), are rarely consumed (Forbes 1888; Fitz 1966; Hoxmeier & DeVries 1997). Large amounts of detritus may be present, especially in empty stomachs, and sand can be present in large amounts, likely the result of a waterborne sand load during high-flow periods (Eddy & Simer 1929; Rosen & Hales 1981).

Gill rakers do not appear on juvenile Paddlefish until they are 60–100 mm TL (2.4–3.9 inches), do not develop for filter feeding until individuals reach 120–170 mm TL (4.7–6.7 inches), and are not fully formed until specimens attain 225–250 mm EFL (8.9–9.8 inches). Therefore small young-of-the-year Paddlefish do not filter feed but selectively feed on large, slow-moving cladoceran zooplankton (Rosen & Hales 1981; Michaletz et al. 1982; Wilkens et al. 1997, 2001, 2002). Water fleas (*Daphnia* spp.) are the most common prey item for juveniles <150 mm TL (5.9 inches) even though they represent only 13% of the zooplankton population, but small zooplankton (*Bosmina* spp.) may be important for larval Paddlefish <20 mm TL (0.08 inch) during early exogenous feeding. Aquatic and terrestrial insects also make up a significant portion of the diet in late summer (Ruelle & Hudson 1977; Chipps et al. 2009). Once juvenile Paddlefish begin filter feeding they capture both slow- and fast-moving zooplankton >0.20–0.25 mm long (0.008–0.01 inch), but consume fast-moving zooplankton in proportions less than their abundance. Juvenile Paddlefish can switch back to particulate feeding if only large prey are available or are in abundance (Rosen & Hales 1981; Michaletz et al. 1982). Filter feeding in young Paddlefish (<300 mm EFL, 11.8 inches) is delayed until after the second growing season when fish densities are low and large preferred prey (chironomids and the Giant Water Flea, *Leptodora kindtii*) are common (Kozfkay & Scarnecchia 2002). Larval Paddlefish can be cannibalistic in culture settings, especially if food supply is too low, but cannibalism also can occur when food is abundant (Yeager & Wallus 1982; Mims & Schmittou 1989; Grande & Bemis 1991).

Seasonal Feeding Periodicity

In the northern part of its range, spring and autumn feeding peaks are apparent in Paddlefish that coincide with greatest abundance of zooplankton and moderate water temperatures. Feeding continues through the winter at low levels, and little to no feeding occurs during the summer (Eddy & Simer 1929; Rosen & Hales 1981). Paddlefish in the mid-South (Kentucky) only have reduced levels of feeding in February (Hageman et al. 1986). Based on stomach fullness, southern populations vary in seasonal feeding. Alabama populations showed no seasonal changes (Hoxmeier & DeVries 1997), but feeding peaked in the summer and winter in Louisiana (Smith et al. 2009b).

Diel Periodicity

Stomach fullness indicates no differences in feeding activity in adult Paddlefish between light and dark periods (Rosen & Hales 1981). Young-of-the-year Paddlefish in main-stem reservoirs and adults in rivers often feed on aquatic insects that only move into the water column at night, which may indicate a preference for nocturnal feeding (Ruelle & Hudson 1977; Hoxmeier & DeVries 1997), and juvenile Paddlefish are only collected in shallow-water habitat at night, presumably while feeding (Allen 1911). Paddlefish move longer distances at night and use shallower areas, suggesting they actively feed at night (Zigler et al. 1999; Paukert & Fisher 2000).

Age and Growth

Paddlefish are typically aged by counting annual growth rings in the lower jaw bone (dentary). This technique works well in Paddlefish in Montana and North Dakota ≤10 years old. Older Paddlefish tend to have their ages underestimated, but dentary ages are still accurate to ±3 years (Scarnecchia et al. 2006). False annual rings (halo bands), which are caused by slow or no growth due to some disturbance or cessation of feeding, decreases accuracy and are more prevalent in southern populations

(Hageman et al. 1986; Scarnecchia et al. 2006). Counting annual growth rings in the leading pectoral fin rays is also used to age Paddlefish when the sacrifice of a large number of specimens is not an option (O'Keefe & Jackson 2009).

Regardless of the inaccuracy of aging, Paddlefish are long-lived fish. Most populations have a median age from 5 to 8 years and a maximum age from about 14 to 18 years (Jennings & Zigler 2009) with one Montana specimen aged at 56 years (Scarnecchia et al. 2007). Northern populations of Paddlefish reach an older age (median 27 years) compared with southern populations (median 11 years) (Paukert & Fisher 2001a). In the upper Missouri River, Montana and North Dakota, mean age of Paddlefish is 25 years and ages >30 years are not uncommon (Scarnecchia et al. 1996b, 2007). Maximum ages reported for Missouri, Oklahoma, and Kentucky are 30, 27, and 21 years, respectively (Purkett 1963a; Timmons & Hughbanks 2000; Scarnecchia et al. 2011). Paddlefish in southern populations are short-lived with a maximum age in Alabama of 12 years, which is younger than age of maturity for some northern populations (Hoxmeier & DeVries 1997; Lein & DeVries 1998; O'Keefe & Jackson 2009). Louisiana Paddlefish live to a slightly older age (14 years) compared with other southern populations (Reed et al. 1992). Shorter lifespans in warmer climates are associated with higher metabolic demands that compress life histories (Scarnecchia et al. 2011). Differences between some populations may be influenced by commercial harvest, which reduces longevity in exploited populations (Alexander et al. 1985; Russell 1986; Hoffnagle & Timmons 1989). Sexual differences can occur with females living longer (mean 28 years) than males (mean 23 years) in a northern population (Scarnecchia et al. 2007) compared with males living longer (11 years) than females (9 years) in a southern population (Lein & DeVries 1998). Maximum age is not different between lotic (rivers) and lentic (reservoirs and lakes) populations (Paukert & Fisher 2001a).

Growth rates for yolk-sac larvae are low as most energy is used for final development of many organ systems, but growth becomes rapid once exogenous feeding begins (Bemis & Grande 1992). Growth in length is extremely rapid during the first year; growth slows through ages 3–5 and much slower rates occur thereafter (Adams 1942; Russell 1986; Reed et al. 1992; Paukert & Fisher 2001a). As growth in length slows, weight gain increases with weight potentially doubling between ages 5 and 10 (Adams 1942; Russell 1986). Because males typically mature earlier than females, their growth rates slow at a younger age. In Kentucky, male growth rates are faster for Paddlefish ≤ age 5, then onset of maturity slows growth and females grow faster thereafter (Hageman et al. 1986). In the upper Missouri River, Montana and North Dakota, male and female Paddlefish have similar growth rates until reaching ages 5–10, then males begin to mature and growth slows, but females continue to grow rapidly and become heavier and longer than similar-aged males (Scarnecchia et al. 2007). This same pattern is present in Oklahoma with males initiating maturation at age 5 (Scarnecchia et al. 2011). Slower growth continues after maturation in Montana and North Dakota until about age 20 for males and age 25 for females, when growth stops or becomes negative (Scarnecchia et al. 2007).

Latitudinal differences in growth rates are evident during the first year of life with slower growth in more northern populations directly related to a shorter growing season and less food availability (Ruelle & Hudson 1977; Reed et al. 1992; Lein & DeVries 1998; Jennings & Zigler 2009). In Montana reservoir populations, Paddlefish only reach an average of 208 mm TL (8.2 inches) at age 1 compared with 296 mm TL (11.7 inches) at the end of the growing season in South Dakota and Nebraska, 456 mm TL (18.0 inches) at age 1 in Tennessee, and 721 mm TL (28.4 inches) at the end of the growing season in Oklahoma (Houser & Bross 1959; Robinson 1966; Ruelle & Hudson 1977; Pasch et al. 1980). Rapid first-year growth also occurs in southern populations within Alabama and Louisiana (Reed et al. 1992; Lein & DeVries 1998).

Habitat differences in growth for young-of-the-year Paddlefish also exist. Lentic populations grow faster compared with lotic populations (Reed et al. 1992; Paukert & Fisher 2001a). The average size for young-of-the-year Paddlefish is 316 mm EFL (12.4 inches) for reservoir and lake populations and 283 mm EFL (11.1 inches) for river populations. Average size of age-1 Paddlefish doubled after the Arkansas River was impounded in Oklahoma (Paukert & Fisher 2001a), and the average size of age-1 Paddlefish in lotic habitat in Alabama averaged only 224 mm EFL (8.8 inches), considerably less than reservoir populations in Alabama (421–461 mm EFL, 16.6–18.1 inches) or lake populations in Louisiana (411–455 mm EFL, 16.2–17.9 inches) (Reed et al. 1992; Hoxmeier & DeVries 1997; Lein & DeVries 1998). These differences are attributed to larger populations of zooplankton in reservoirs and lakes, summer temperatures exceeding optimal growing temperatures in riverine backwaters and oxbows (Russell 1986; Hoxmeier & DeVries 1997; Paukert & Fisher 2001a), and reduced energy expenditures in a slow-current or current-free environment (Jennings & Zigler 2009). Exceptional growth rate and year-class strength are attributed to extraordinary rain events or cessation of drought conditions leading to elevated reservoir levels and extremely large zooplankton blooms (Houser & Bross 1959; Houser 1965; Scarnecchia et al. 2009). Growth rates between these lentic and lotic habitats are similar for older-aged (age 2+) Paddlefish (Paukert & Fisher 2001a).

Seasonal growth in age-1 Paddlefish is variable within and between populations. Growth in the Alabama River is most prominent in spring and early summer with little growth from August to February (Hoxmeier & DeVries 1997). Substantial winter growth of 65–90 mm (2.6–3.5 inches) occurred in a Tennessee reservoir (Pasch et al. 1980), but little growth over winter (<50 mm, 2.0 inches) occurred in an Oklahoma reservoir (Houser & Bross 1959).

Population Sizes and Densities

All populations of Paddlefish are now fragmented and have suffered a decline in numbers of individuals. The size and density within a given population can vary greatly. Estimates of population size and abundance of adults for large river reservoirs are relatively low (3,421–13,000 Paddlefish; <1/ha), most mortality being caused typically by sport and commercial harvest (Alexander et al. 1985; Hageman et al. 1986; Paukert & Fisher 2001a). Where fishing pressure is low or absent abundance can be much higher, with 3,541 Paddlefish (2.6/ha) in a small impoundment in Alabama and 1,689 Paddlefish (8.8/ha) in a subimpoundment of a large reservoir in Tennessee (Boone & Timmons 1995; O'Keefe & Jackson 2009). Densities of Paddlefish in an oxbow lake along the lower Alabama River were also high with 13.1 individuals/ha (419 individuals) (Hoxmeier & DeVries 1997). Population size of Paddlefish in rivers also can vary greatly with an estimate of 1,353 Paddlefish occupying the Wisconsin River (Runstrom et al. 2001) and 25,118 in the Neosho River (Combs 1982).

Natural mortality of adult Paddlefish may be quite low (Rosen et al. 1982), and this is the case in an unexploited population in a subimpoundment of a Kentucky reservoir with only 9% annual mortality (Boone & Timmons 1995). But annual mortality rates of unexploited populations can be quite high in river, lake, and reservoir populations (26–48%/year). These high estimates may be in part from other human-induced mortality (unintentional snagging, boat collisions) or the lasting effects of past commercial fisheries before moratoriums were implemented (Reed et al. 1992; Hoxmeier & DeVries 1997; Paukert & Fisher 2001a; Runstrom et al. 2001; O'Keefe & Jackson 2009). Annual mortality rates in exploited Paddlefish populations range from moderate to high (18–69%) with exploitation accounting for 7–>50% of mortality even though the suggested maximum exploitation rate is ≤15% (Combs 1982; Rosen et al. 1982; Bronte & Johnson 1985; Hoffnagle & Timmons 1989; Timmons & Hughbanks 2000; Scholten & Bettoli 2005; Donabauer et al. 2009). Overall mortality rates tend to be lower in lotic habitats (Paukert & Fisher 2001a).

Energetics

Gonadal fat bodies are amassed in both sexes during immature growth periods. Increase in fecundity in young adults, indicated by gonadal weight relative to body weight, is accompanied by a decrease in gonadal fat bodies. In Montana and North Dakota, fat reserves in males are gradually depleted over several spawns, but in females reserves are rapidly depleted after two or three spawns by age 25. Fecundity remains steady after reserves are spent, but females show a drop in reproduction after age 35 (Scarnecchia et al. 2007). Gonadal fat bodies in Oklahoma Paddlefish are lower in relative weight, and thus have diminished energy storage due to a greater metabolic demand from higher regional temperatures (Scarnecchia et al. 2011). Energetic tradeoff may affect migratory behavior with younger Paddlefish migrating farther upstream than older individuals (Scarnecchia et al. 2007).

Predation

Early life stages of Paddlefish are susceptible to predation. In culture ponds aquatic insects prey on larval Paddlefish, and juveniles are preyed on extensively by numerous vertebrates, especially birds (Graham et al. 1986; Mims et al. 2009). Large Channel Catfish (*Ictalurus punctatus*) prey on juvenile Paddlefish in polyculture settings (Tidwell & Mims 1990). In reservoirs juvenile Paddlefish are found in the stomachs of Walleye (*Sander vitreus*) and Sauger (*Sander canadensis*), which co-occur in pelagic habitats with Paddlefish (Mero et al. 1994; Parken & Scarnecchia 2002). In reservoir ranching, stocked Paddlefish fingerlings are preyed on by Largemouth Bass (*Micropterus salmoides*) (Onders et al. 2001).

Parasites

Numerous parasites are found in Paddlefish, including protozoans (2 species), jellyfish (1), flukes (7), flatworms (3), nematodes (6), leeches (1), and copepods (1). Parasites occur in all Paddlefish life stages, including pre-spawned eggs (jellyfish). Some parasite species are only known from Paddlefish (Hoffman 1999; Raikova 2002; Pracheil et al. 2005; Bullard et al. 2008). Although not typically considered in the parasite literature, lampreys heavily parasitize Paddlefish. In Wisconsin ≤96% of Paddlefish can be infected by Silver Lampreys (*Ichthyomyzon unicuspis*); individual Paddlefish can have ≤25 Lampreys attached and 28 fresh wounds (Wagner 1908; Lyons 1993; Cochran et al. 2003).

CONSERVATION

Paddlefish are highly vulnerable to anthropogenic activities that block migratory routes, destroy crucial habitat, and overharvest adults because of their life history characteristics, habits, and valuable eggs (Boreman 1997; Graham 1997b; Wilson & McKinley 2004). The peripheral range of the Paddlefish has shrunk with the extirpation of Great Lakes populations in Canada and the United States, Mississippi River basin populations in four states (Maryland, New York, North Carolina, and Pennsylvania), and several western Gulf Coast drainages, and most extant populations are far below historical levels (Carlson & Bonislawsky 1981; Gengerke 1986; Parker 1988; Williamson 2003). In 1989 the U.S. Fish and Wildlife Service (USFWS) was petitioned to list the Paddlefish as Threatened (USFWS 1990) but a status review determined that listing was not warranted; however, it was classified as a Category 2 species, which indicated it is of concern and merits additional data to assess its status. This category was discontinued by USFWS, and now the Paddlefish has no federal status (USFWS 1992, 1996; Jennings & Zigler 2000). Although the Paddlefish occupies most of its historical range and most populations appear to be stable or increasing, overharvest, river modifications, altered land use in riparian areas, and pollution are still a concern (Jennings & Zigler 2000; Bettoli et al. 2009b; Gerken & Paukert 2009). Paddlefish are considered Vulnerable or of Special Concern in the southeastern United States and throughout their range and are protected from harvest in 12 states (Williams et al. 1989; Warren et al. 2000; Jelks et al. 2008; Bettoli et al. 2009b; IUCN 2011).

Conservation Action and Regulation

The Paddlefish is a wide-ranging species that occurs in 22 states and has commercial harvest, sport harvest, or both in more than half of these. Historically many states have had no or poor reporting of fisheries activities for the species. This resulted in varied and opposing management strategies across the range of the Paddlefish where integrated multijurisdictional reporting and management should have been used to preserve or recover Paddlefish populations (Carlson & Bonislawsky 1981; Graham & Rasmussen 1999; Rasmussen 1999; Henley et al. 2001; Léonard et al. 2004). In response to this need, the Mississippi Interstate Cooperative Resource Association (MICRA) was formed in 1989 to better manage Paddlefish within the Mississippi River basin, and MICRA has evolved into a multiagency organization that coordinates resource management on an array of aquatic organisms. Even though MICRA has no regulatory authority and relies solely on the voluntary cooperation of its members, interjurisdictional management of Paddlefish has improved and most Paddlefish populations are stable or increasing, but limited consistency still exists in regulations among states (Rasmussen 1999; Williamson 2003; Bettoli et al. 2009b; Hansen & Paukert 2009; Scholten 2009). With the worldwide interest in Paddlefish products, especially caviar, and the sharp decrease in caviar production globally, international management of Paddlefishes is needed and is performed under the Convention on International Trade of Endangered Species (CITES). CITES is founded on the voluntary participation of >160 countries to control international trade. Under CITES, all Acipenseriformes are listed as Appendix I (threatened with extinction) or Appendix II (uncontrolled trade might threaten their existence) species, requiring permits and certifications for international trade involving the Paddlefishes and Sturgeons, along with additional initiatives for their protection, especially against illegal trade. The listing of all Acipenseriformes by CITES has resulted in better monitoring and control of international trade of these species, but questions remain about its effectiveness to ensure that international trade is not detrimental for four species, including the Paddlefish (Raymakers 2002; Raymakers & Hoover 2002; Léonard et al. 2004; Pikitch et al. 2005; IUCN 2011).

Fishery Exploitation and Conservation

Because Paddlefish co-occur in large numbers, have predictable spawning runs, and congregate in deep water areas

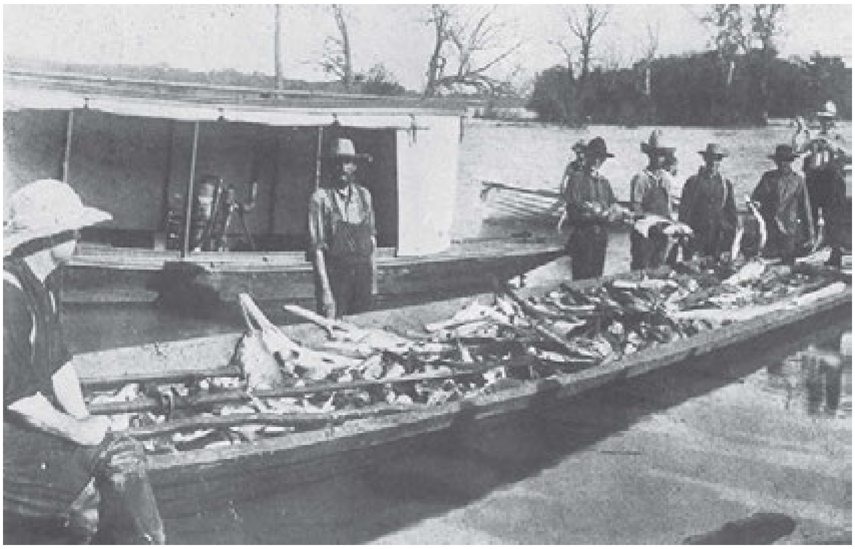

Figure 6.18. A 3,175 kg (7,000 pound) catch of Paddlefish, *Polyodon spathula* (from Forbes & Richardson 1920).

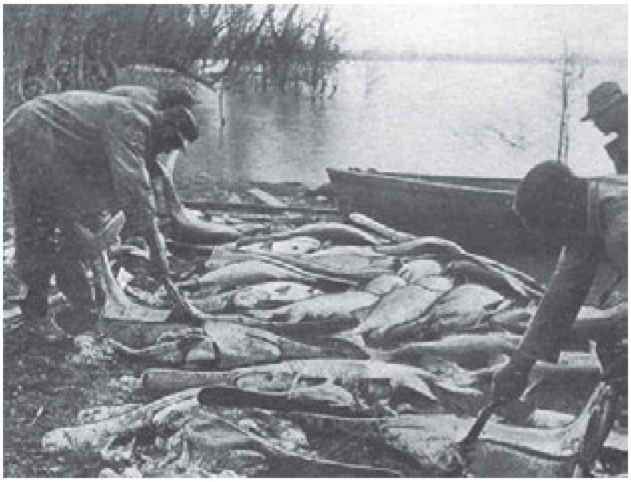

Figure 6.19. Cutting up and removing roe from Paddlefish, *Polyodon spathula*, caught in Moon Lake, Mississippi (from Hussakof 1911).

in the winter, they are easy to locate and harvest. But most populations cannot support high levels of exploitation because of relatively low recruitment and growth rates, delayed maturation, reaching a harvestable size before maturation, and the lack of annual spawning by females. These factors are compounded by the predominance of roe (eggs) fisheries for Paddlefish that target large, gravid females that are crucial for successful spawning (Pasch & Alexander 1986; Jennings & Zigler 2000; Scholten 2009). Paddlefish stocks were depleted in many floodplain lakes by the early 1900s in the lower Mississippi River basin because of the demand for their caviar as a substitute for Sturgeon caviar and the ease of capturing Paddlefish with seines in these backwater habitats (Figs. 6.18 and 6.19) (Stockard 1907; Hussakof 1911; Alexander 1914). Although roe of Paddlefish was not as prized as its flesh in the upper Mississippi River basin at that time, concerns were raised that populations would soon become decimated, perhaps even to the point of extirpation (Wagner 1908; Coker 1923). The Paddlefish industry began to wane almost as soon as it started with many fishers in the early 1900s no longer fishing for Paddlefish because of decreasing numbers and the extensive nets needed to effectively catch Paddlefish (Stockard 1907). Overexploitation in concert with channelization and dam construction has led to a 95% decline in harvest of Paddlefish in the Mississippi River basin (Coker 1929; Carlson & Bonislawsky 1981; Gengerke 1986). In general exploitation rates of ≤15% of the adult population/year are estimated as acceptable for maintaining a stable population (Combs 1982; Jennings & Zigler 2000). Regulations imposed on commercial and sport fisheries, including limits (creel, quota, size, and slot), closed seasons, gear restrictions, and prohibition on high grading, as well as sanctuaries and closures, are intended to prevent overharvest and protect brood stock. Some populations have increased due to more conservative regulations and better monitoring by state agencies, especially for sport harvest. Unfortunately, many states have poor or no reporting requirements, most states do not know if regulations help meet these objectives, and several regulations are known to be ineffective (Combs 1986; Elser 1986; Scarnecchia et al. 1989; Graham 1997; Scholten & Bettoli 2005, 2007; Gordon 2009; Hansen & Paukert 2009; Mestl & Sorensen 2009; Quinn 2009). Even with detailed stock assessment and scientifically sound regulation recommendations, enacted regulations are often a compromise with the commercial fishing industry (Bettoli et al. 2007). Paddlefish do not exhibit sexual dimorphism so both males and females are sacrificed as fishers look for roe. The demand for caviar remains high as Sturgeon stocks continue to decline worldwide. As a result, demand continues to grow for roe from North American Acipenseriformes, including Paddlefish, and increasing legal, but overly exploitative, and illegal commercial harvest will continue as a threat (Graham & Rasmussen 1999; Jennings & Zigler 2000; Pikitch et al. 2005; Bettoli et al. 2007; Gordon 2009; Quinn et al. 2009).

Aside from the obvious affects of harvest on Paddlefish populations, unintentional mortality can arise from commercial and sport fisheries bycatch. Paddlefish are obligate ram ventilators that must swim continually to ventilate their gills, and capture in commercial gear causes inadequate gas exchange (Burggren & Bemis 1992). When Paddlefish come in contact with nets and are no longer able to ram ventilate they make little effort to escape, quickly losing equilibrium and floating belly up (Stockard 1907; Hussakof 1911), the result of poor gas exchange when switching to inadequate buccal pumping (Burggren & Bemis 1992). Mortality can occur from even minimal handling (Lyons 1993). In commercial gillnet fisheries for Paddlefish roe, bycatch rate can be high (92% sublegal-sized fish, legal-sized males, and immature females) and significant mortality can occur (50%). Fishing monofilament nets (versus multifilament) and fishing at temperatures >10°C (50°F) (especially >17°C, 62.6°F) increases mortality (Bettoli & Scholten 2006; Quinn et al. 2009). Intentional mutilation is another problem in commercial fisheries because some fishers cut Paddlefish to check for eggs (Quinn et al. 2009). In tailwater fisheries severe tissue damage can affect 16–36% of a population from snagging hooks, lines, and boat propellers, including injury or loss of paddles, although mortality from snagging may be low (Rosen & Hales 1980; Hesse & Mestl 1993; Lyons 1993; Scarnecchia & Stewart 1997). Mortality also can occur from collecting Paddlefish for research. Gillnet mortality can be as high as 92% when water temperatures are >21°C (69.8°F), decreases to <15% mortality at <18°C (64.4°F), and are lowest at temperatures <10°C (50°F) (Paukert & Fisher 2001a; Scholten & Bettoli 2005). Minimal delayed mortality (4%) occurred in captured and tagged Paddlefish after 2 weeks (Kerns et al. 2009). In contrast delayed mortality of 34% occurred 3 days after Paddlefish were gillnet captured and tagged, but this was in association with reservoir destratification (Boone & Timmons 1995). Mortality of 35% has also occurred with hoop nets (Dieterman et al. 2000), and electrofishing mortality can range from 5 to 15% (Lyons 1993; Hoxmeier & DeVries 1997; Lein & DeVries 1997).

Dams

Paddlefish face formidable barriers created by some dams that can block access to spawning grounds and fragment formerly contiguous populations, threatening genetic integrity and viability (Unkenholz 1986; Wilson & McKinley 2004). Microsatellite data suggest that Paddlefish populations were previously more connected before gene flow was restricted by dams (Heist & Mustapha 2008). Dams also cause Paddlefish to congregate in tailwater areas, especially during upstream spawning migrations in the spring (Rehwinkel 1978; Rosen et al. 1982; Southall & Hubert 1984; Moen et al. 1992). This makes spawning Paddlefish extremely vulnerable to harvest (Coker 1923; Rehwinkel 1978; Carlson & Bonislawsky 1981; Rosen et al. 1982; Miller & Scarnecchia 2008; Donabauer et al. 2009). Paddlefish will migrate upstream through fully opened dam gates of low-head dams during high river discharge, but not if dam gates are partially closed because of the high water velocities (>3.0 m/s, 9.8 feet/s). Because migrating Paddlefish are guided by flowing water they typically congregate mid-river just below dams. Most lock chambers are downstream of these areas and lack attracting flows, so even if lock gates are fully open they typically do not function as passage for spawning migrations (Coker 1929; Southall & Hubert 1984; Zigler et al. 2004). The electroreceptive paddle used by Paddlefish to locate zooplankton is affected negatively by metal objects (see behavior section). Sensitivity to electrical current produced by metallic objects in water could interfere with migration through locks and dams (Jørgensen et al. 1972; Wilkens et al. 1997, 2002; Gurgens et al. 2000), but some success of upstream movement through locks occurs when attraction flows (1,463 m^3/s, 4,800 $feet^2/s$) are present overnight (Mettee et al. 2009).

Dams also degrade or eliminate habitat or cues for spawning and habitat for early life history stages (Unkenholz 1986; Gerken & Paukert 2009). Cold hypolimnetic releases from deep reservoirs delay spawning for 20 days to 1 month compared with warmer releases or unimpounded rivers and may lower recruitment given the shorter growing season available to progeny (Wallus 1986a; Braaten et al. 2009a). Cold releases also may prohibit Paddlefish from spawning in otherwise suitable habitat (Pasch et al. 1980). Dams are used extensively for flood control and as such severely mute high water events in systems with multiple dams, so substantial water rises to initiate spawning are present only in large-scale floods (Wallus 1986a). Dams also reduce suspended sediments and turbidity, which makes embryos and larvae more susceptible to predation and removes a spawning cue for adults. Dams and associated channelization have eliminated backwaters and oxbow lakes, critical habitats used by Paddlefish as feeding and nursery areas (Stockard 1907; Russell 1986; Hoxmeier & DeVries 1997; Firehammer & Scarnecchia 2006; Miller & Scarnecchia 2008; Clark-Kolaks et al. 2009). Subimpoundments off of large reservoirs are artificial equivalents of backwaters and oxbow lakes and should be protected from sport and commercial harvest (Boone & Timmons 1995).

Avenues for Paddlefish dispersal between drainages were created with large-scale modifications to rivers. The Tennessee-Tombigbee Waterway artificially connects the Tennessee River to the Tombigbee River and the rest of the Mobile Basin, threatening the genetic integrity of the unique Mobile Basin population (DeVries et al. 2009).

Although the overall effects of dams and accompanying channelization are detrimental to Paddlefish populations, robust reproducing populations can become established in reservoirs when adequate riverine spawning habitat is available in tributaries (Carlson & Bonislawsky 1981; Gengerke 1986; Sparrowe 1986; Paukert & Fisher 2001a; Scarnecchia et al. 2009). Negative effects downstream of dams can be mitigated by artificially increasing water releases from dams that can boost spawning migration and reproductive success of Paddlefish (Elser 1986; Miller & Scarnecchia 2008). But increased flows are typically alternated with lower discharge in regulated systems, creating favorable conditions for commercial fishers to effectively use gillnets (Scholten & Bettoli 2005).

Pollution

Paddlefish are large, long-lived fish with high lipid content, and they can accumulate organochlorine and heavy metal contaminants in their flesh and gonads that can interfere with early life stage development, reduce plasma steroid levels, and cause chronic health problems. Contaminants are likely taken up by ingesting contaminated suspended sediments while filter feeding. Paddlefish in the Ohio River have high levels of organochlorine in gonads, especially in testes and immature eggs due to their higher lipid content relative to mature eggs. Female Paddlefish have a lower total organochlorine body burden compared with males, probably due to elimination of a significant amount of contaminants by releasing large masses of eggs during spawning relative to the small amount of milt released by males. Based on histological examination of organs, Paddlefish in the Ohio River may be experiencing immunosuppression, hepatic metabolic disorders, and altered neuroendocrine function due to organochloride exposure, jeopardizing long-term health (Gundersen et al. 2000). In that population, Paddlefish fillets and mature eggs exceeded the U.S. Food and Drug Administration's action limits for chlordane (>0.3 ppm) (Gundersen & Pearson 1992; Gundersen et al. 1998, 2000). Mercury contamination in the Mobile Basin in 1970 negatively impacted the Paddlefish market in that area (Carlson & Bonislawsky 1981), and Paddlefish flesh exceeded the U.S. Environmental Protection Agency reference dose for methylmercury for unrestricted consumption in the Ohio River; older Paddlefish had higher concentrations ≤0.53 ppm (Dasgupta et al. 2004). Altered land use in riparian areas has increased nonpoint source pollution and sedimentation in rivers. Increased siltation is a threat to the spawning habitat of Paddlefish, which need clean, hard substrates to deposit eggs for proper aeration and development of embryos (Purkett 1961; Russell 1986; Gerken & Paukert 2009).

Industrial Use of Waterways

Juvenile Paddlefish are susceptible to entrainment during industrial water use and channel dredging. During a 12- and 10-month period, >4,000 and >9,000 young-of-the-year Paddlefish were impinged on intake screens at one water intake facility in a Tennessee reservoir (Pasch et al. 1980). Laboratory experiments show that entrainment of juvenile Paddlefish <115 mm EFL (4.5 inches) is likely within a radius of 1.25 m (4.1 feet) of the cutterhead of dredges used to maintain navigation channels. It is not known whether Paddlefish would detect the metal cutterhead through electroreception before entrainment, if detection would allow them to successfully disperse from the area, or if their response would be a U-turn, increasing the likelihood of entrainment (Hoover et al. 2009b).

All life stages of Paddlefish are impacted from commercial vessel passage. Larvae are highly vulnerable to stranding when commercial vessel drawdown and subsequent dewatering of littoral zones are simulated in a laboratory setting. Larvae are positively rheotactic (swim toward current) and are more likely to swim toward the shoreline as water recedes (Adams et al. 1999b). Larval Paddlefish are also susceptible to propeller-induced shear stress because their internal organs are underdeveloped and integument is fragile. Mortality of ≤49% occurred in Paddlefish larvae in laboratory experiments replicating shear stress from vessels (Killgore et al. 2001). Juvenile Paddlefish (249–318 mm EFL, 9.8–12.5 inches) leave areas as barge traffic approaches and do not return until the barge is >2 km (1.24 mile) away. This avoidance behavior may be caused by the metal hull of the barge and sediment plumes created by the propellers interfering with the electroreception of Paddlefish or by Paddlefish hearing receptors being sensitive to sonic emissions from propellers (Barry et al. 2007). Adult Paddlefish can be entrained by towboat propellers, and once entrained, have a high probability of being struck by a propeller due to their large size. The threat of entrainment is increased in narrow, shallow, and sluggish reaches of rivers, and higher propeller speeds increase risk of a propeller strike (Killgore et al. 2011).

Invasive Species

Paddlefish are at high risk for threats from invasive species because they are already exposed to numerous anthropogenic stressors and occur in large rivers of the central United States where many invasive species are becoming established. Potential negative effects of invasive species on Paddlefish include direct competition for resources, vectors for the spread of disease or parasites, and more subtle effects such as altering of the food web. The main conflict is competition for resources, especially for food (zooplankton) and habitat, with the largest threat from filter-feeding Asian carps, which have showed exponential population growth over the last decade (Pegg et al. 2009). In experimental ponds young-of-the-year exotic Bighead Carp (*Hypophthalmichthys nobilis*) outcompeted similar-aged Paddlefish for zooplankton by either feeding more quickly or efficiently or through aggressive behavior, resulting in a lower growth rate for Paddlefish. Although their gill rakers are similar in size and function, Bighead Carp can produce mucus on their gill rakers to trap smaller food items, giving them an ecological advantage over Paddlefish (Schrank et al. 2003). In adult Paddlefish little diet overlap exists with exotic Bighead Carp and Silver Carp (*H. molitrix*) in the Illinois and Mississippi Rivers; the Asian carps primarily consume small rotifers and Paddlefish prefer large crustacean zooplankton. But rotifers were the dominant zooplankton during this study, and diet overlap may be realized if rotifers are in low abundance (Sampson et al. 2009). Pelagic Threadfin Shad (*Dorosoma petenense*) and Alewife (*Alosa pseudoharengus*) introduced as forage fishes outside of their native range also may compete with Paddlefish for zooplankton. Nonnative White Perch (*Morone americana*) introduced from the eastern United States and Round Gobies (*Neogobius melanostomus*) established in the Great Lakes from Eurasia and threatening to invade the Mississippi River basin are possible predators on Paddlefish embryos. Two introduced rhabdoviral diseases that are potential threats to Paddlefish are viral hemorrhagic septicemia and spring viremia of carp. Parasites from Asian carps that are of greatest concern as potential Paddlefish threats include the Asian Carp Tapeworm (*Bothriocephalus acheilognathi*) and the Anchorworm (*Lernaea cyprinacea*). Change in size and population dynamics of plankton in the food web are indirect effects of introduced Asian carps on Paddlefish, and plankton densities have decreased dramatically following Zebra Mussels (*Dreissena polymorpha*) becoming established, which could direct energy flow from the water column to the benthos. Eradication projects and barriers erected to restrict movement of invasive species may have negative impacts on Paddlefish, such as bycatch mortality and restricting migration (Pegg et al. 2009).

Artificial Propagation and Stocking

Discussions of propagating Paddlefish to augment depleted populations first began in the early 1900s (Alexander 1914), but Paddlefish eggs were not fertilized and hatched artificially until 1961 (Purkett 1963b). Stocking can be used to offset destruction of spawning habitat, supplement exploited populations, or reestablish extirpated populations of Paddlefish. Ten states have hatchery stocking programs (Graham 1997; Williamson 2003; Bettoli et al. 2009b). Oklahoma is using stocking to reestablish an extirpated population, and South Dakota and West Virginia consider stocking to play an important role in maintaining or improving the status of Paddlefish. Pennsylvania and New York are attempting to reestablish Paddlefish, but no evidence of natural reproduction is as yet documented (Argent et al. 2009; Bettoli et al. 2009b; Grady & Elkington 2009). Paddlefish stocks were moved among drainages in stocking efforts before 2000, which raised legitimate conservation concerns because genetic structuring exists among populations and mixing could lead to reduced fitness through outbreeding depression. Concern continues to exist about decreasing the genetic diversity of a population through stocking. This has occurred in Paddlefish populations by using insufficient numbers of brood stock or by having variation in male reproductive success lead to differential production (Epifanio et al. 1996; Jennings & Zigler 2000; Heist & Mustapha 2008; Grady & Elkington 2009; Sloss et al. 2009). Aquaculture for meat and caviar products is also a conservation tool because it will hopefully lead to reduced fishing pressure on wild Paddlefish populations (Billard & Lecointre 2001).

Global Climate Change

Paddlefish populations will be negatively affected by the predicted impacts of global climate change on river ecosystems in temperate North America. Reduced precipitation and flow, increased frequency of droughts, and more extreme floods will likely exacerbate many of the existing threats to Paddlefish and their habitats (Gerken & Paukert 2009). If climate warms, metabolic demands will increase for all populations of Paddlefish, which in turn will compress the life history of this species and lead to an overall shorter lifespan, including a shorter prime reproductive period. Given that southern populations of Paddlefish already have a narrow window for reproductive success, these populations may become non-viable as global temperatures increase (Scarnecchia et al. 2011).

COMMERCIAL IMPORTANCE

Commercial Fisheries

Paddlefish were only eaten locally until the late 1800s when a commercial fishery for their flesh and roe began as Lake Sturgeon (*Acipenser fulvescens*) and Atlantic Sturgeon (*Acipenser oxyrinchus*) stocks were depleted. Next to Sturgeons, Paddlefish had the highest market value of any fish in the Mississippi River basin, even though the Paddlefish caviar industry, which began in 1896, was prominent only in the lower Mississippi River (Goode 1884; Beard 1878; Townsend 1902; Wagner 1908; Forbes & Richardson 1920; Eddy & Simer 1929). The eggs were sold for caviar as a substitute for Sturgeon roe, the boneless flesh was dried or smoked and sold as Sturgeon, and the heads and fins were sometimes boiled for oil (Stockard 1907; Hussakof 1911; Alexander 1914; Coker 1930). The greatest harvest of Paddlefish was 1,105 mt (1,218 tons) in 1899 with the vast majority from the Mississippi River. Due to extreme levels of exploitation and habitat alteration from channelization and construction of dams, overall Paddlefish harvest decreased by 40% in 1903, held steady in 1922, then dropped by 32% in 1931 (Coker 1929; Carlson & Bonislawsky 1981; Gengerke 1986; Pasch & Alexander 1986). But in some instances river systems that were fragmented by a series of reservoirs (Tennessee, Cumberland, and Arkansas Rivers) had an increase in Paddlefish populations, with the Tennessee River system supporting the largest commercial harvest of Paddlefish from 1950 through at least the 1970s (Carlson & Bonislawsky 1981; Gengerke 1986). Because of reduced imports of Sturgeon flesh during World War II, harvest increased temporarily with 324 mt (357 tons) harvested from just 2 Alabama reservoirs in 1942. Harvest again declined from the 1950s to mid-1970s with many commercial fishers discarding Paddlefish roe from 1965 to 1975 because it only brought $0.55–$4.41/kg ($0.25–$2.00/pound). Even when the price of salted Paddlefish roe increased to $26.46–$33.07/kg ($12–$15/pound) in 1979 after the United States stopped importing Iranian caviar, many fishers were unaware of the developing market and still discarded roe. But in 1980–1981 Paddlefish roe was bringing $44.09–$55.12/kg ($20–$25/pound), and >340 mt (375 tons) of dressed Paddlefish were harvested in the Tennessee, Cumberland, and Alabama River systems in 1980. Roe prices reached a high of $110/kg ($49.90/pound) in 1985 (Alexander & Peterson 1982; Pasch & Alexander 1986; Semmens & Shelton 1986; Hoffnagle & Timmons 1989; Hoxmeier & DeVries 1996). As Paddlefish populations were reduced in these areas, commercial fishers began exploiting Paddlefish populations in Louisiana (Reed et al. 1992). The price and harvest of Paddlefish roe continue to be affected by the availability of Sturgeon caviar (Hoffnagle & Timmons 1989), but since the worldwide catch of Sturgeons decreased sharply in the 1990s, demand continues to grow for products from North American Acipenseriformes, including Paddlefish (Pikitch et al. 2005).

As of 2006, commercial fishing for Paddlefish was allowed in 7 of 22 states with extant Paddlefish populations; 6 of these allow harvest when roe is present in females (Bettoli et al. 2009b, Quinn 2009; Scholten 2009). From 2000 to 2006 the mean annual commercial harvest of Paddlefish included 487,600 kg (1,074,974 pounds) of flesh (47,400 fish) and 25,380 kg (55,953 pounds) of processed roe, which is much higher than reports from 1965–1975 and 1992 (Carlson & Bonislawsky 1981; Graham 1997; Quinn 2009). The majority of harvest came from Arkansas, Kentucky, and Tennessee with the Ohio River producing the most Paddlefish flesh and Kentucky Lake (Tennessee River) producing the most roe (Scholten & Bettoli 2005; Quinn 2009). The demand and prices for Paddlefish products continue to grow. A market for smoked Paddlefish flesh is developing and recent prices for roe have doubled with roe selling for \$154–>\$200/kg (\$69.85–\$90.72/pound) wholesale and \$381–\$1,340/kg (\$172.82–\$607.82/pound) retail (Pikitch et al. 2005; Scholten & Bettoli 2005, 2007; Bettoli et al. 2009b).

Nets are the most efficient method to commercially harvest Paddlefish. When a Paddlefish makes contact with a net, it makes feeble efforts to free itself and can be removed by hand with little struggle (Stockard 1907; Alexander 1914; Coker 1923). In the early 1900s, 3.2 km (2 miles) seines, 9.1 m (30 feet) deep, were used to capture Paddlefish in backwaters and floodplain lakes in the lower Mississippi River basin by encircling an area >1.6 km (1 mile) in circumference and hauling in the seine on a huge reel by the crew walking up the spokes of the wheel (Fig. 6.20) (Stockard 1907; Hussakof 1911). Another method involved dragging a 183 m (600 feet) seine between 2 boats near the surface up and down a lake all day with a row boat moving along the seine every 0.5 h to remove Paddlefish from the net (Alexander 1914). Drifting trammel nets were used in rivers to capture Paddlefish concentrated below dams (Coker 1923). Currently fishers typically use large-meshed gill and trammel nets (127–152 mm bar mesh, 5–6 inches) to harvest Paddlefish, which are effective (Quinn 2009). Two fishers harvested 5,443 kg (12,000 pounds) in 2 nights in a subimpoundment of a reservoir (Semmens & Shelton 1986). Gillnets cannot be easily deployed in riverine sections of reservoirs when discharge is high. The number of Paddlefish harvested in Kentucky Lake is positively related to the number of fishable days in a season, with greater harvest in drought years (Scholten & Bettoli 2005).

Sport Fisheries

Most sport fisheries for Paddlefish developed after construction of dams on rivers. Paddlefish concentrating in tailwaters below dams provide a substantial fishery. Those populations that support a self-sustaining fishery are in the upper and central Mississippi River basin. Paddlefish harvested are typically immature, but a few sport fisheries concentrate on adult Paddlefish during spawning migrations. Large harvest coincides with high spring flows (Carlson & Bonislawsky 1981; Combs 1982; Rosen et al. 1982). Tailwater fisheries can be affected by power generation negatively since low flows decrease Paddlefish abundance, especially over weekends when energy demands are low (Unkenholz 1986).

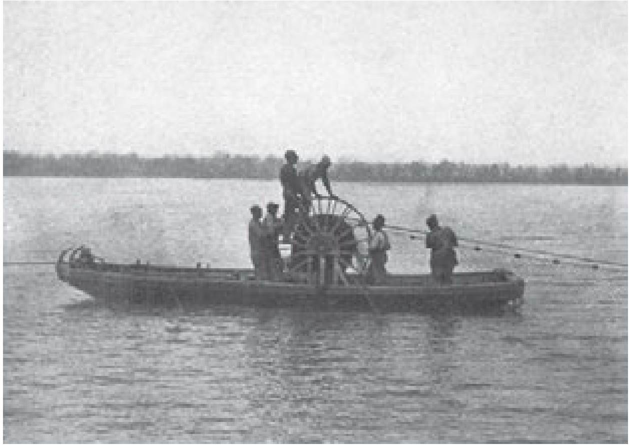

Figure 6.20. Huge reel mounted in a flat-bottomed boat winding up a seine to catch Paddlefish, *Polyodon spathula*, by the crew walking up the spokes of the wheel (from Hussakof 1911).

Because Paddlefish are zooplanktivores they do not take bait, so snagging is the only common method used in recreational harvest. Snagging involves jerking a large treble hook and a lead weight through the water on a heavy line with a stout spinning rod and reel (Purkett 1963a; Scarnecchia et al. 1996a; Hansen & Paukert 2009). Although Paddlefish incur injury when snagged, hooking mortality may be low and a catch-and-release sport fishery is feasible (Scarnecchia et al. 1996a; Scarnecchia & Stewart 1997). A small archery fishery also exists (Rosen & Hales 1980). As of 2006, sportfishing for Paddlefish is allowed in 14 of 22 states with extant Paddlefish populations (Bettoli et al. 2009b; Hansen & Paukert 2009). From 2000 to 2006 annual sport harvest of Paddlefish ranged between 15,000 and 20,000, with 7 fisheries harvesting >1,000 Paddlefish annually (Quinn 2009).

Aquaculture

Artificial propagation of Paddlefish is used for stocking to enhance sport and commercial fisheries, reestablishing extirpated populations, and raising Paddlefish outside of North America for harvest. The preferred method of rearing young Paddlefish is to stock larvae in heavily fertilized ponds, which promotes dense growth of zooplankton. Polyculture in ponds with Channel Catfish and other fishes also is used, with excess food replacing fertilizer to promote zooplankton growth (Graham et al. 1986; Semmens & Shelton 1986; Mims et al. 2009). Paddlefish also can be raised in tanks and trained to eat an artificial diet of sinking pellets, but they switch to filter feeding on zooplankton when placed in ponds or reservoirs (Graham et al. 1986; Kroll et al. 1992, 1994; Mims 2001). In China, Paddlefish are raised in floating cages with an artificial diet for production of flesh (Mims et al. 2009). Paddlefish were successfully established in an Ozark reservoir by stocking fingerlings, and a sport fishery was realized in 10 years (Graham 1986). A commercial fishery for Paddlefish can be created by stocking fingerlings in small reservoirs and harvesting in <2 years; this extensive culture program is referred to as reservoir ranching (Onders et al. 2001; Williamson 2003). Although female Paddlefish do not produce eggs until age 7 and they must be sacrificed for caviar production, mature females produce large quantities of highly valuable eggs (about 15% of their body weight a large female is worth >$650) (Mims 2001; Bettoli & Scholten 2006; Bettoli et al. 2007). To increase caviar yields attempts are being made to produce all-female (monosex) populations of Paddlefish for culture, which involves gynogenesis (producing embryos containing only maternal chromosomes), steroid-induced sex reversal of some individuals to produce neomales (produce only X-determinant sperm), and the use of these neomales to produce all-female progeny (Mims & Shelton 1999). Paddlefish were introduced into the former Soviet Union and Europe beginning in 1974 for aquaculture in ponds, and demand for live Paddlefish and eggs has continued overseas. Paddlefish are now part of polyculture systems for meat and caviar in several European, Middle Eastern, and Asian countries (Hoover 1999; Billard & Lecointre 2001; Vedrasco et al. 2001; Lobchenko et al. 2002; Hubenova et al. 2007; Mims et al. 2009).

LITERATURE GUIDE

Several sources provide excellent overviews on the Paddlefish in North America. These include edited volumes and books that cover many aspects of Paddlefish biology, management, propagation, and conservation (Dillard et al. 1986; Hochleithner & Gessner 1999; LeBreton et al. 2004; Paukert & Scholten 2009) and those that focus on harvest and conservation (Williamson et al. 1999; Williamson 2003).

Acknowledgments

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Chapter 7 Lepisosteidae: Gars

Anthony A. Echelle and Lance Grande

Living Gars are easily identified by their torpedo-shaped bodies encased in hard, rhombohedral-shaped scales, their posteriorly set median fins, and their elongate bills lined with sharply pointed teeth. Today's Gars (order Lepisosteiformes) include seven species, five in eastern North America and one each in Cuba and the tropics of Central America. They are living fossils in the sense of Hubbs & Lagler (1958:30) and Wiley & Schultze (1984). That is, the family is ancient (Gars are >100 million years old), the living species show numerous primitive neopterygian traits, and the closest relatives are extinct. The living-fossil status and the air-breathing habit of Gars have generated a great deal of interest among fish systematists, developmental and evolutionary biologists, and physiologists.

Gars are sometimes considered undesirable, a view fueled by their reputation for competing with and consuming more desirable gamefishes, their potential for fouling commercial fishing nets, and sometimes even the perception that the larger species pose a threat to humans (Scarnecchia 1992; Spitzer 2010). Most of the perceived problems posed by Gars are minor relative to the negative reactions they often receive from fishers and, until rather recently, most state and federal fishery management programs (Scarnecchia 1992; Spitzer 2010).

Gars are now beginning to be appreciated for their own sake and as integral components of healthy aquatic ecosystems. As top predators they perform ecosystem functions that may be important in stabilizing populations of gamefish and their prey (Cross 1967; Scarnecchia 1992). At the same time, their unusual, prehistoric appearance makes Gars valued attractions at public zoos and aquaria. This is particularly true for the larger species, one of which, the Alligator Gar, *Atractosteus spatula*, reaches about 3 m TL.

DIVERSITY AND DISTRIBUTION

The Gars inhabit waters of eastern and central North America, Meso-America, and Cuba (Figs. 7.1 and 7.2). The fossil record extends the time range of the Lepisosteidae to >100 mya and extends the geographic range to western North America, Europe, Africa, India, and South America. Gars, particularly Alligator Gars, occasionally occur in coastal brackish or marine habitats, but the extant Gars are effectively freshwater fishes (Table 7.1). The same appears true for fossil Gars, which are almost entirely known from freshwater deposits (Grande 2010).

The living Gars are placed in two genera: *Lepisosteus* with four species (Figs. 7.3 and 7.4) and *Atractosteus* with three species (Fig. 7.5). The extant members of *Lepisosteus* are restricted to eastern North America from Montana and Texas eastward. The distribution of *Lepisosteus osseus* (Longnose Gar, Aguja in Mexico) includes southern Quebec, Canada, south to Florida and northern Mexico, and westward from the Great Lakes region to Montana. The Longnose Gar is also referred to vernacularly as the common Gar, billfish, and needlenose Gar. *Lepisosteus oculatus* (Spotted Gar, Catán Pinto in Mexico) occurs from the Great Lakes south to the Gulf Coast of Texas, northern Mexico, and east to northwestern Florida. *Lepisosteus platyrhincus* (Florida Gar, Florida spotted Gar in earlier literature) is restricted to Florida and lowlands of southern Georgia. *Lepisosteus platostomus* (Shortnose Gar, vernacularly known as the duckbill garfish) occurs in low-gradient regions of the Mississippi River basin, from northeastern Texas north to Montana, east to Ohio, and south to Mississippi.

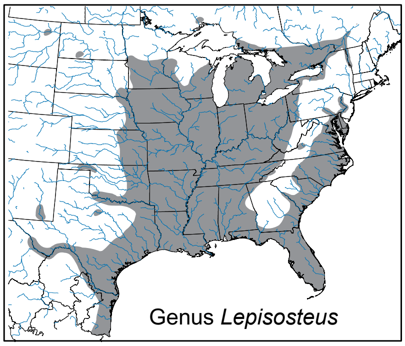

Figure 7.1. Geographic range of *Lepisosteus*.

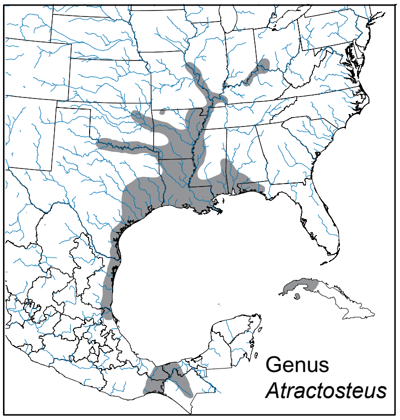

Figure 7.2. Geographic range of *Atractosteus*.

Table 7.1. Life history characteristics of Gars, Lepisosteidae.

Characters	Characteristics	Comments
Number of extant species	Seven in two genera	*Lepisosteus*, four species *Atractosteus*, three species
Salinity preferences	Fresh and brackish waters	Alligator Gar occasionally in full-strength sea water
Maximum size recorded in m TL	Alligator Gar, 3 Cuban Gar, 2 Longnose Gar, 1.6 Others, 1.1–1.3	Females larger than males
Maximum age	Alligator Gar, 50 years Longnose Gar, 32 years Others, <20 years	Females live longer than males
Age at first reproduction	Males, 2–6 years; females, 2–10 years	
Size at first reproduction	0.3–1.4 m TL	Females larger than males
Iteroparous or semelparous	Iteroparous	Annual breeding season
Fecundity estimates (ovarian counts)	Alligator Gar, 157,000 Tropical Gar, about 50,000 Longnose Gar, 18,000–33,000 Others, 2,500–13,000	Varies greatly with body size
Mature egg diameter	About 3 mm	
Egg deposition sites	Vegetation; bottom substratum	Scattered in a small area
Clutch size	Unknown	Probably 100s to 1,000s
Range of spawning dates	United States, February–June Mexico, May–September Costa Rica, April–October	In United States, latitudinal shift toward later seasons
Habitat of spawning sites; average water depth	Shallow (<1 m), usually quiet water with vegetation	Longnose Gar often on open, rocky-bottom lake shores
Incubation period	2–10 days or more	Depends on temperature
Mean size at hatching	About 8 mm TL	
Parental care	None	
Major dietary items	Fish, crayfish, shrimp, insects	Earliest feeding stage: microcrustaceans and insects
General year-round habitat	Bayous, swamps, rivers, lakes, tidal creeks and lagoons, estuaries	
Migratory or diadromous	Generally not migratory, or some degree of potamodromy	Longnose Gar migrate up streams to spawn, but migration is not obligatory
Imperilment status	Most species reasonably secure; Alligator Gar Vulnerable to extirpation from much of its range; some species extirpated from peripheral portions of their ranges.	Overharvest and anthropogenic loss of habitat and habitat connectivity implicated in declines of Alligator Gar

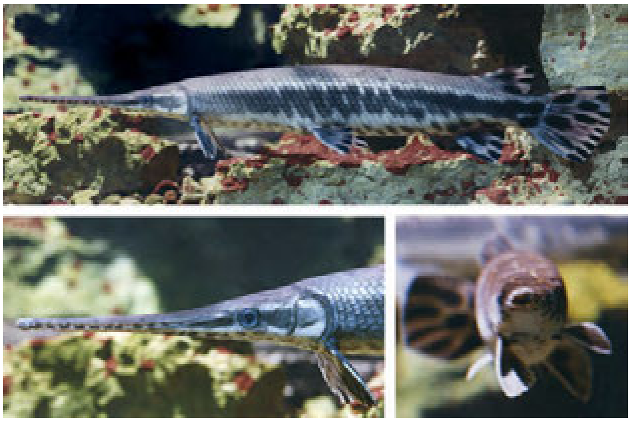

Figure 7.3. Longnose Gar, *Lepisosteus osseus*. Two aquarium specimens, each about 730 mm TL (used from Grande 2010 with permission of the American Society of Ichthyologists and Herpetologists). *Top and lower left*, same individual.

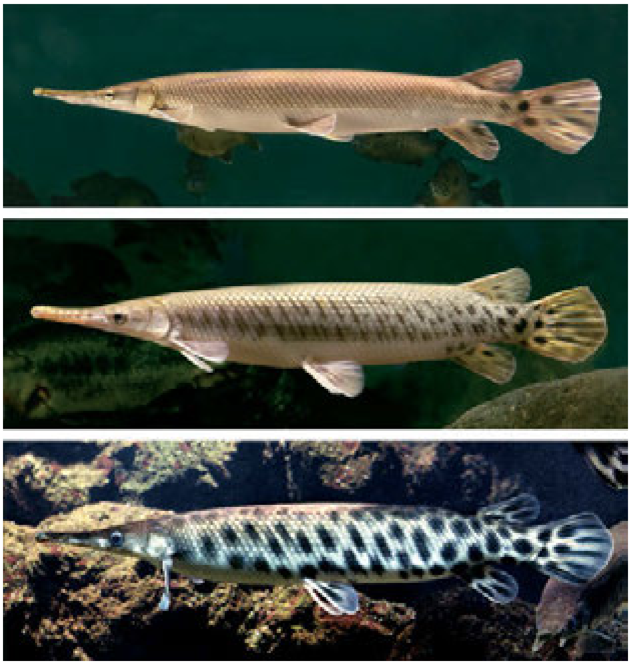

Figure 7.4. Other living species of *Lepisosteus*. *Top*: Shortnose Gar, *L. platostomus*, about 520 mm TL. *Middle*: Spotted Gar, *L. oculatus*, about 480 mm TL. *Bottom*: Florida Spotted Gar, *L. platyrhincus*, about 500 mm TL. All were aquarium-held individuals (used from Grande 2010 with permission of the American Society of Ichthyologists and Herpetologists).

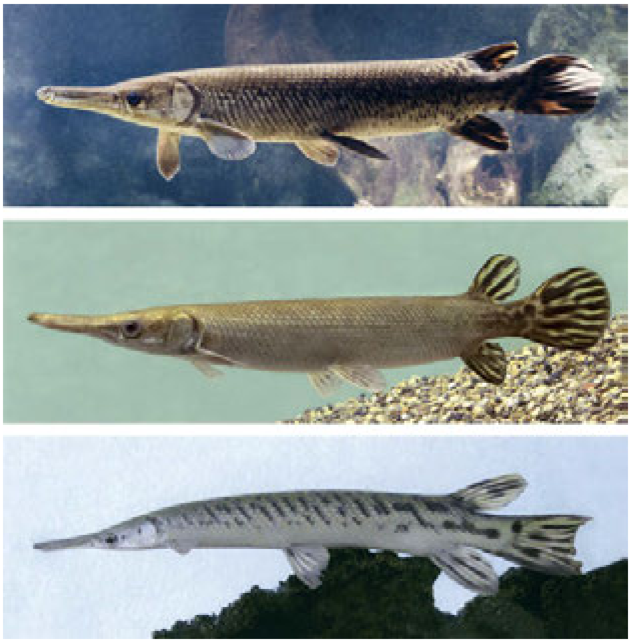

Figure 7.5. Living species of *Atractosteus*. *Top*: Alligator Gar, *A. spatula*, about 780 mm TL. *Middle*: Cuban Gar, *A. tristoechus*, about 400 mm TL. *Bottom*: Tropical Gar, *A. tropicus*, about 450 mm TL. All were aquarium-held individuals (used from Grande 2010 with permission of the American Society of Ichthyologists and Herpetologists).

Extant members of *Atractosteus* occur in North America, Central America, and Cuba. *Atractosteus spatula* (Alligator Gar, Catán in Mexico) occurs in North America from Vera Cruz, Mexico, north through the Mississippi River drainage into southern Illinois, Indiana, and Ohio and along much of the Gulf Coast. *Atractosteus tristoechus* (Cuban Gar, Manjuarí in Cuba) is known from western Cuba and the nearby Isle of Pines. *Atractosteus tropicus* (Tropical Gar; Pejelagarto) occurs from southern Mexico and Central America with disjunct populations in Atlantic and Pacific drainages of Mexico and Central America (Miller et al. 2005).

Gars as Non-Natives

The Shortnose Gar in Wisconsin is the only well-documented example of established (naturally reproducing) populations of non-native Gars. The first Wisconsin record was from Lake Winnebago in 1962 (Priegel 1963). The species now is established in the Fox and Wolf Rivers and lower Green Bay of Wisconsin (Fuller et al. 1999; Fuller 2011). This range extension probably originated with dispersal from the Mississippi River basin to the Great Lakes basin by way of the artificially constructed Wisconsin-Fox canal (Becker 1983). The ecological effects are unknown.

Other North American records of non-native Gars primarily consist of transient occurrences of single or a few individuals that failed to establish populations. These

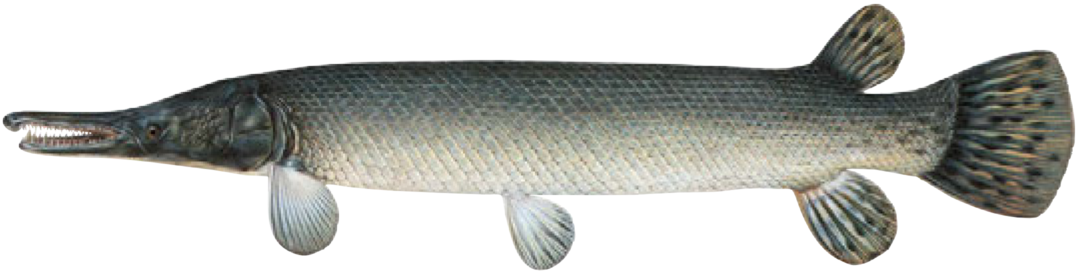

Plate 7.1. Alligator Gar, *Atractosteus spatula*

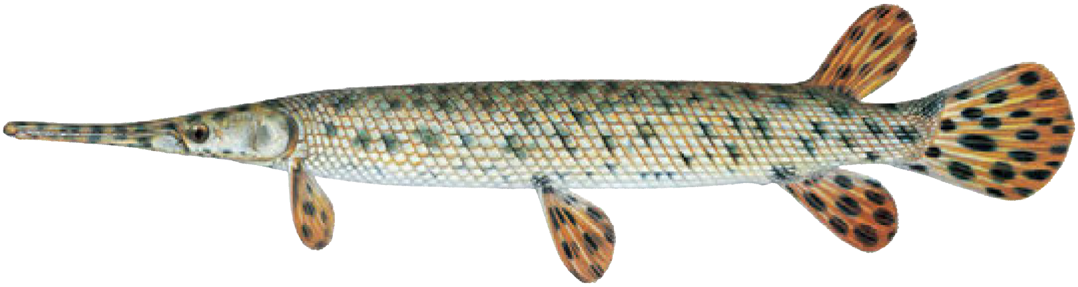

Plate 7.2. Spotted Gar, *Lepisosteus oculatus*

include the Florida Gar in Ontario, Canada, the Spotted Gar in Massachusetts and New York, the Alligator Gar in California (Fuller & Nico 2011), and a Florida Gar in Oregon (McGarvey & Hughes 2008). The population status represented by a South Carolina record of an Alligator Gar from Lake Wateree in 2010 is unknown (Fuller & Nico 2011).

Gars occasionally show up far from their native ranges because of aquarist activity and the sportfishing industry. For example, a single specimen of *Atractosteus* sp. was collected from the Caspian Sea in 2008 (Salnikov 2009), Spotted Gars are reported from China (Ma et al. 2003), and records of individual Alligator Gars from two localities in Malaysia were mentioned in the Singapore media (Asia-One News) in 2008. Conceivably the Malaysian records are a byproduct of the sportfish industry in Thailand. The Alligator Gar is “frequently seen” in Thailand (Chavalit 2005:114), where it was released into recreational fishing lakes and is a sportfishing attraction in fishing guides and advertisements. No published information seems to exist on the reproductive status of these populations.

PHYLOGENETIC RELATIONSHIPS

The phylogenetic position of Gars was part of a classic problem in fish systematics. The groups of controversial relationship were Gars (Lepisosteiformes), Bowfins (Amiiformes), and teleosts (Teleostei). These three groups form the basal branches of the Neopterygii, and resolution of their relationships is important for understanding the transition from primitive actinopterygians (Ray-finned Fishes) to the Teleostei, the group containing nearly all living bony fishes. In early classifications, Gars were placed with the Bowfin (*Amia calva*, Amiidae) in the Holostei, which most ichthyologists considered the sister-group of Teleostei (Müller 1845; Huxley 1861; Regan 1923; Goodrich 1930; Jarvik 1959, 1980; Nelson 1969a; Wiley 1976; Jollie 1984).

More recently, Holostei (Gars + Bowfins) was considered non-monophyletic. This was based primarily on morphological characters thought to be shared by Bowfins and teleosts (Teleostei) but absent in Gars (Patterson 1973; Wiley 1976; Lauder 1980; Lauder & Liem 1983; Gardiner et al. 1996). From the mid-1970s until recently, nearly all systematic ichthyologists using morphological characters have endorsed non-monophyly for the Holostei (Grande & Bemis 1996) with the majority of studies indicating a monophyletic Halecomorphi (Bowfins + Teleostei), although some support existed for a Gars + Teleostei group that was sister to Bowfins (Olsen 1984; Olsen & McCune 1991).

By the 1990s, most molecular systematics studies were indicating a monophyletic Holostei (Gars + Bowfins) rather than a monophyletic Halecomorphi (Normark et al. 1991; Venkatesh et al. 2001; Inoue et al. 2003; Li et al. 2008). Some of these suggested a sister relationship between chondrosteans (Sturgeons, Ascipenseridae, and

Paddlefishes, Polyodontidae) and the Holostei (Venkatesh et al. 2001; Inoue et al. 2003). Later molecular studies supported a monophyletic Neopterygii (Gars + Bowfins + teleosts). These included an analysis of entire mitochondrial DNA sequences and 4 nuclear gene sequences (Hurley et al. 2007) and an analysis of 10 nuclear gene sequences (Li et al. 2008). The former study weakly suggested a sister relationship between the Bowfin and the Teleostei, but the latter provided strong support for a monophyletic Holostei (Gars + Bowfins) that is sister to Teleostei.

The question of holostean relationships became a classic example of molecular data directly conflicting with morphological data (Grande 2010). But then the morphological evidence supporting a monophyletic Halecomorphi (Bowfins + Teleostei) was discovered to be flawed (Grande 2010). Characters thought to be uniquely derived for Bowfins and teleosts but lacking in Gars were found in species of the extinct Gar family †Obaichthyidae. Once corrected, the morphological data set agreed completely with the molecular data in supporting a monophyletic Holostei that is sister to the Teleostei.

The sister relationship between *Lepisosteus* and *Atractosteus* is supported in phylogenetic analyses of morphological data sets encompassing both fossil and extant Gars (Wiley 1976; Grande 2010). In a recent analysis, *Lepisosteus* included the four extant species of the genus and two fossil species (Grande 2010; Fig. 7.6). The Longnose Gar was resolved as sister to a Spotted Gar + Florida Gar clade and the Shortnose Gar was depicted as basal to a clade comprising the other extant species and the two fossil members of *Lepisosteus*. For *Atractosteus*, the Alligator Gar and Cuban Gar formed a clade in an unresolved polytomy that includes the Tropical Gar and four fossil species. The extinct genera †*Cuneatus* and †*Masillosteus* were successively basal members of the Lepisosteidae (Fig. 7.6). A clade comprising the two remaining genera of the order Lepisosteiformes, †*Obaichthys* and †*Dentilepisosteus* (both family †Obaichthyidae), was sister to the Lepisosteidae. The inferred relationships among living Gars agreed with Wiley's (1976) morphological analysis.

The one molecular phylogenetic analysis of the living Gars resolved a tree that differed from the morphological results by placing the Shortnose Gar as sister to the Longnose Gar rather than as the basal member of the group (Fig. 7.6; Wright et al. 2012). The trees for a mitochondrial gene (COI) and a nuclear sequence (S7 intron) were well resolved, and both placed the Shortnose Gar with the Longnose Gar separate from a clade comprising the Spotted Gar and the Florida Gar. The trees for six protein-coding nuclear sequences gave less resolution, but all trees resolved the genera *Atractosteus* and *Lepisosteus* as separate clades. A tree based on the complete molecular data set differed from the tree from morphology only in the aforementioned placement of Shortnose Gar.

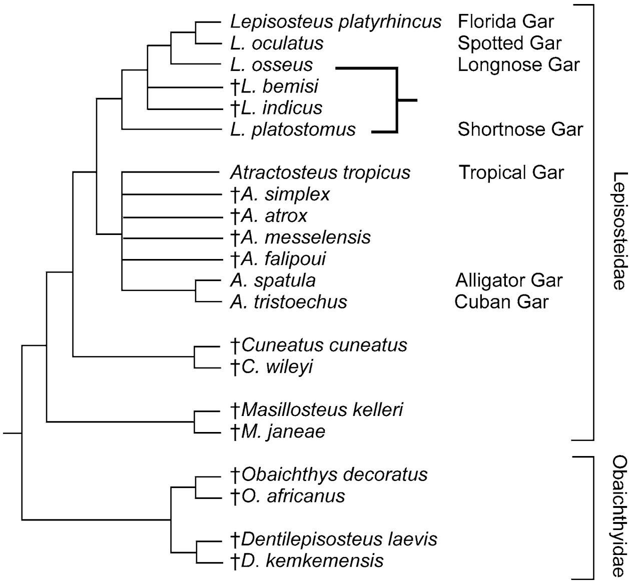

Figure 7.6. Cladogram showing inferred relationships among extant and extinct Gars (order Lepisosteiformes) (used from Grande 2010 with permission of the American Society of Ichthyologists and Herpetologists). The subtree with thicker lines shows the one difference between this morphologically based tree and a tree based on molecular data for the living Gars (i.e., a sister relationship between Shortnose Gar, *Lepisosteus platostomus*, and Longnose Gar, *Lepisosteus osseus*) (Wright et al. 2012).

FOSSIL RECORD

The fossil record of Gars (order Lepisosteiformes) extends as far back as 100–110 mya in the Early Cretaceous (Grande 2010). The fossils, which are numerous in many Mesozoic and Cenozoic deposits, typically consist of isolated scales and vertebrae, both of which are highly diagnostic of the group, as well as partial skeletons (Grande 2010). Whole-body fossils are known from the Cretaceous of Brazil and Africa (100–110 mya) and the Paleogene of North America and Germany (about 55–45 mya). The fossils extend the geographic range of Lepisosteiformes well beyond modern-day borders to include Wyoming, Utah, Alberta, Ellesmere Island, the High Canadian Arctic, Europe, Africa, Madagascar, India, and South America.

The record includes 18 currently recognized species: 15 extinct species, fossil records for 3 extant species (Table 7.2), and 2 fossils of indeterminate taxonomy (potentially undescribed species, 1 each in *Lepisosteus* and *Atractosteus*). Twenty-six nominal species of fossil Gars are of doubtful validity (Grande 2010).

The extensive fossil record of Gars is sometimes overinterpreted. Gar scales and vertebrae are both resilient to wear and decomposition. Consequently, geographic and stratigraphic range data for Gars at the taxonomic level of family (Lepisosteidae) and order (Lepisosteiformes) are extensive. But the majority of this material cannot be unambiguously assigned to genus or species. Much of this relatively undiagnostic material was invalidly named and assigned to genera or even living species based on geographic occurrence or inadequate diagnosis.

Not all Gar fossils are fragmentary and undiagnosable. Some consist of complete, well-preserved skeletons (Fig. 7.7) that are important in understanding the phylogenetic history of Neopterygii and the ecological breadth of Lepisosteiformes. Grande (2010) gives detailed descriptions of all fossil Gar species currently considered valid. Some of the fossil species from western North America belong to the extant Gar genera and others belong to extinct genera (Fig. 7.7).

Interestingly, all well-preserved fossil species of *Lepisosteus* and *Atractosteus* occur outside the present geographic range of Lepisosteidae. Valid fossil species of the two extant (living) Gar genera include †*Lepisosteus bemisi*, †*Atractosteus simplex*, and †*Atractosteus atrox*, all from the 52 million-year-old freshwater limestone deposits of southwestern Wyoming; †*Lepisosteus indicus* from 65 million-year-old freshwater deposits of India; †*Atractosteus messelensis* from 48 million-year-old deposits of Germany; and †*Atractosteus falipoui* from 100 million-year-old deposits of Morocco. The oldest known occurrence of fossil material assignable to *Lepisosteus* (not assigned to species) is from 75 million-year-old deposits of Alberta, Canada.

Fossil lepisosteid Gars in North America also include two specialized, short-snouted extinct genera appearing to have had an ecological niche different from that of Gars living today. These forms are well represented by beautifully preserved complete skeletons from the Late Paleocene

Table 7.2. The geographic and temporal distribution of fossil Gars (Lepisosteiformes) recognizable at the level of genus (Grande 2010). The ages shown encompass the entire known time span for the order Lepisosteiformes. Indet. = indeterminate (assignable to genus but not to species; potentially an undescribed species). Superscripted 1 = assignment to species tenuous (Grande 2010).

Species	**Geography**	**Period/Epoch**	**Age (mya)**
Lepisosteus osseus	Kansas, North Carolina,^{1} United States	Pleistocene	<2.5
Lepisosteus platostomus	Kansas,^{1} Florida,^{1} United States	Pleistocene	<2.5
Lepisosteus platyrhincus	Florida,^{1} United States	Pleistocene	<2.5
†*Lepisosteus bemisi*	Wyoming, United States	Early Eocene	52*
†*Lepisosteus indicus*	Central Province, India	Late Cretaceous or Early Paleocene	~65
†*Lepisosteus* indet. sp. A	Alberta, Canada	Late Cretaceous	~75
Atractosteus spatula	Kansas,^{1} Texas,^{1} Florida,^{1} United States	Early Pliocene and Pleistocene	<5
†*Atractosteus simplex*	Wyoming, United States	Early Eocene	52*
†*Atractosteus messelensis*	Germany	Early Middle Eocene	<50, >45
†*Atractosteus atrox*	Wyoming, United States	Early Eocene	52*
†*Atractosteus falipoui*	Morocco	Early Cretaceous	~100
†*Atractosteus* indet. sp.	Alberta, Canada	Late Paleocene	<60, >55
†*Cuneatus cuneatus*	Wyoming, United States	Early Eocene	~50–55
†*Cuneatus wileyi*	Wyoming, United States	Early Eocene	~50–55
†*Masillosteus kelleri*	Germany	Early Middle Eocene	<50, >45
†*Masillosteus janeae*	Wyoming, United States	Early Eocene	52*
†*Obaichthys decoratus*	Ceará, Brazil	Early Cretaceous	~110
†*Obaichthys africanus*	Morocco	Cretaceous	~100
†*Dentilepisosteus laevis*	Ceará, Brazil	Early Cretaceous	110
†*Dentilepisosteus*(?) *kemkemensis*	Morocco	Early Cretaceous	100

* Date for Fossil Butte Member revised in Grande (2013).

through Early Eocene (about 55–52 mya) and include †*Cuneatus cuneatus* and †*Cuneatus wileyi* from Utah and †*Masillosteus janeae* from Wyoming (Fig. 7.7). The genus †*Cuneatus* had tiny jaw teeth, a short head, and a short body. The genus †*Masillosteus* had short, strongly ossified jaws and a mouth containing, on the coronoids and vomer, pads of flattened crushing teeth suited for feeding on mollusks and arthropods. The †*Cuneatus* and †*Masillosteus* lineages are not known to have survived past the Middle Eocene (about 48 mya).

Another important group of extinct fossil Gars is the †Obaichthyidae (sister to Lepisosteidae). These Gars are known from several well-preserved skeletons (detailed in Grande 2010). The family includes two species from eastern Brazil (†*Obaichthys decoratus* and †*Dentilepisosteus laevis*) and two from western Morocco (†*Obaichthys africanus* and †*Dentilepisosteus kemkemensis*). All known †obaichthyid Gars are from Cretaceous deposits about 100–110 mya. The trans-Atlantic distribution of †obaichthyids is a clear reflection of the African-South American connection that existed during part of the Cretaceous.

MORPHOLOGY

More than two centuries ago, Linnaeus placed the Longnose Gar with Pikes (Esocidae) in the teleostean genus *Esox* (Wiley 1976). The Pike-like attributes of Gars include soft-rayed fins with no spines, jaws extended into bills, and elongate, torpedo-shaped bodies with posteriorly positioned dorsal and anal fins (Figs. 7.3–7.5, 7.7). Even so, Gars are easily distinguished from *Esox* and all other North American fishes by their relatively rigid scale-jacket (skin) with thick ganoid scales and from all except the Bowfin by their abbreviate-heterocercal caudal fin. Other features include large body size (1–3 m TL); coloration drab with no marked sexual differences; breeding tubercles absent; lateral line complete; cephalic mechanosensory canal system well developed; pectoral fins low on body; pelvic fins mid-abdominal; eyes large and round; jaws lined with sharply pointed teeth and extended into an elongated bill; and upper jaw extended slightly past lower jaw and terminating in a fleshy bulge containing the paired olfactory organs.

Pigmentation

Adult Gars are various shades of brown to olive-green dorsally and white to cream-colored ventrally. Spotted Gars and Florida Gars have well-defined, roundish dark spots on the body and head including the bill. The other Gars can have dark markings, possibly in response to light conditions, but often are rather uniformly pigmented. The fins generally are pale yellowish with dark spots.

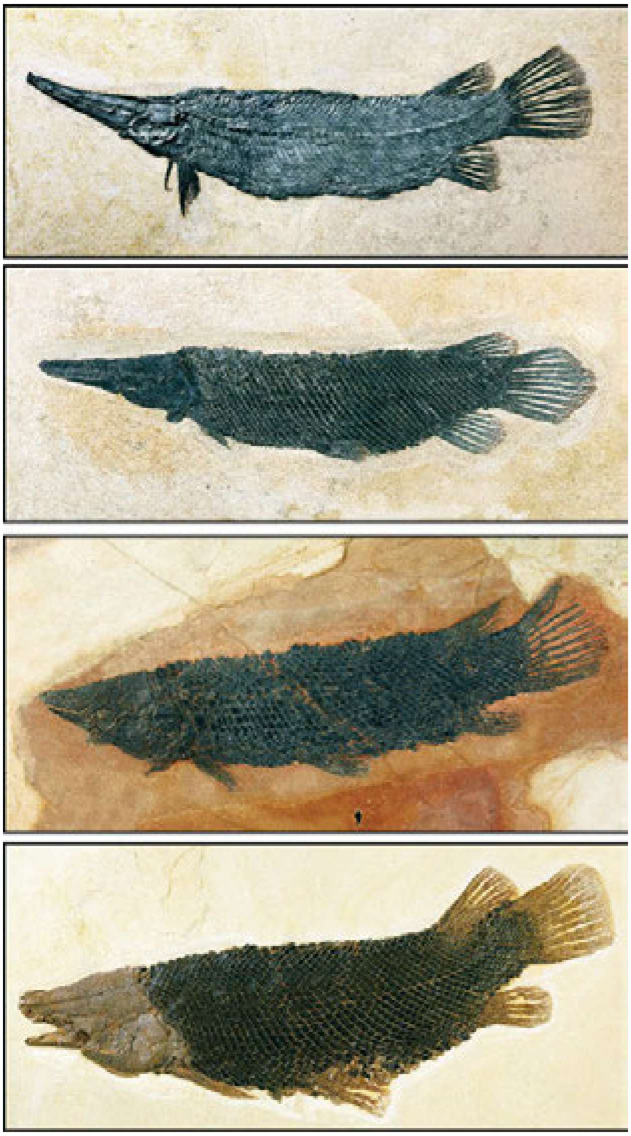

Figure 7.7. Examples of extinct species of *Lepisosteus* and *Atractosteus* and extinct genera †*Cuneatus* and †*Masillosteus* of short-headed Gars. *From top to bottom*: †*L. bemisi* (730 mm TL, Peabody Museum specimen PU 14585), †*A. simplex* (674 mm TL, Field Museum PF12597), †*C. cuneatus* (346 mm TL, British Museum BMNH P.61229), and †*Masillosteus janeae* (945 mm TL, Field Museum PF15196). †*L. bemisi*, †*A. simplex*, and †*M. janeae* are from the 52-million-year-old Fossil Butte Member of the Green River Formation, Wyoming; †*C. cuneatus* is from the 55-million-year-old Flagstaff Member of the Green River Formation, Utah (used from Grande 2010 with permission of the American Society of Ichthyologists and Herpetologists).

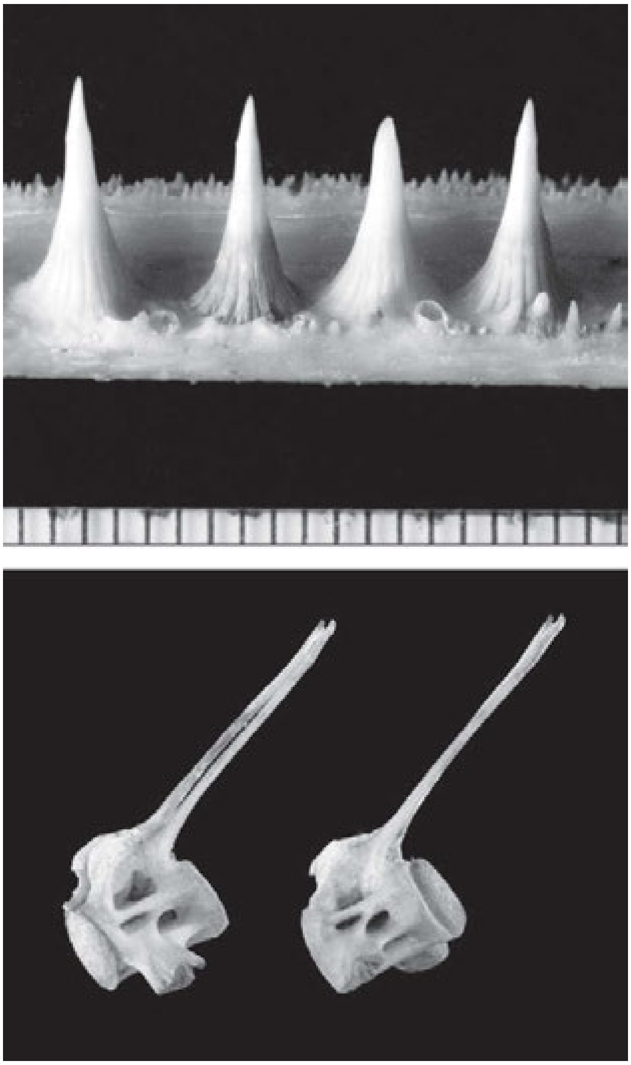

Figure 7.8. Diagnostic characters of Gars. *Top*: Plicidentine tooth structure. Note the deep longitudinal striations or "folded" appearance at the base of the four large fangs. *Bottom*: Vertebrae from an adult Alligator Gar, *Atractosteus spatula*, showing the opisthocoelous centra characteristic of Lepisosteiformes. Left vertebra tilted to show the convex anterior end of centrum, right vertebra tilted to show the concave posterior end of centrum.

Environmentally induced melanism (unusually black individuals) occurs in Florida Gars, Spotted Gars, and Alligator Gars (Suttkus 1963). A relatively high frequency (5%) of melanism in a James River, Virginia, Longnose Gar population was based on density, not dispersion, of melanosomes, indicating a genetic basis (Woolcott & Kirk 1976). An individual from an Oklahoma population of Spotted Gar was dull white with a pale yellowish tinge (Tyler 1994) and a xanthic (yellow-gold) Florida Gar has been reported (David 2009). These individuals were not complete albinos because the eyes had black pigment.

Size

Gars can be unusually large for freshwater fishes. Alligator Gars sometimes reach 3 m TL and 137 kg, and there is a report of a 3.7 m TL individual (Suttkus 1963; Ross 2001). The congeneric Tropical Gar is much smaller with a maximum of 1.3 m TL (Mora et al. 1997) and a typical length of ≤1 m TL (Mendoza et al. 2010a). Longnose Gars are often >1 m TL and can reach 1.6 m TL and a weight of 19 kg; Spotted Gars, Florida Gars, and Shortnose Gars typically are ≤1 m TL with maximum recorded lengths of 1,092 and 1,067 mm TL for Spotted Gars and Shortnose Gars, respectively (Suttkus 1963; Ross 2001).

Living Fossils with Derived Characters

Gars have a number of features present in Paleozoic ancestors (>250 mya) but lost in most modern fishes. The most obvious such traits are thick, ganoid scales covering the body and an abbreviate-heterocercal caudal fin—that is, caudal-fin ray supports (hypurals and some of the haemal spines) attach to the upturned ventral surface of the vertebral column. Another primitive character is that the leading edges of the fins are strengthened by a biserial row of modified scales (fulcra).

A number of more recently derived morphological traits arose in the ancestral lepisosteid Gar (Grande 2010). These include the following, among 13 others (Grande 2010): absence of the interopercular bone, one of four plates in the opercular series of most modern fishes; a tongue-like structure supported by several bony basihyal plates sometimes referred to as the tongue bone; plicidentine teeth (folded walls of dentine at the base); and opisthocoelous vertebrae (Fig. 7.8). Opisthocoelus vertebrae are convex on the anterior side of the centrum and concave on the posterior side.

Atractosteus versus *Lepisosteus*

Morphological differences between *Atractosteus* and *Lepisosteus* can be summarized as follows (Grande 2010). The symphysis between the two halves of the lower jaw in *Lepisosteus* occurs along the medial surface of the anterior right and left dentary with anterior ends pointing anteriorly. In *Atractosteus*, the symphysis occurs between the anterior ends of the dentary, which are curved medially to meet each other at their ends. The total gill raker count on the left first arch is <40 in *Lepisosteus* and >50 in *Atractosteus*. The gill rakers are small, pear-shaped bones bearing tiny conical teeth in *Lepisosteus*, and in *Actractosteus* they are in long, densely packed rows and have ornate, deeply serrated edges. Finally, the width-to-length proportion of the frontal bone of the cranium ranges from 0.12 to 0.28 in *Lepisosteus* and 0.22 to 0.34 in *Atractosteus*.

Urogenital System

The right and left ovaries but not the testes are staggered in the body cavity and located mostly anterior and posterior to the pelvic fins, respectively (Suttkus 1963). In two studies the left ovary was consistently larger and carried more eggs (Longnose Gar, Netsch & Witt 1962; Spotted Gar, Redmond 1964), but no such difference was noted in Spotted Gars from Lake Ponchartrain (Love 2004). The ureters (Wolffian ducts) from the kidneys and the genital ducts connect separately to a common urogenital sinus that opens to the outside just posterior to the anus (Jaroszewska & Dabrowski 2009).

Alimentary Canal and Organs of Taste and Smell

The alimentary canal includes a short esophagus, a well-defined stomach, a cluster of pyloric caecae at the anterior end of the intestine and on the wall of the posterior intestine, and a spiral fold, all of which are present by the time the yolk sac is absorbed (Jaroszewska et al. 2010). The spiral fold has been referred to as "a remnant of the spiral valve" (Suttkus 1963:64), a primitive trait that increases the surface area for absorption of digestive products.

Taste buds occur in the floor of the pharynx and on the external surface of the head (Song & Northcutt 1991a). The distribution and innervation of the external taste buds appear to be a derived trait uniting Gars, the Bowfin, and the other neoteleosts (Song & Northcutt 1991a). The tip of the upper jaw has a pair of olfactory sacs, each with separate incurrent and excurrent openings.

Mechanosensory Canals and Pit Lines

Gars have a system of external organs (neuromasts) that detect water movement relative to the surface of the fish. The system is similar in general aspect to that of the Bowfin and most teleosts (Song & Northcutt 1991ab; Grande 2010) and includes mechanosensory pit lines and canals (Fig. 7.9). In pit lines, neuromasts are in shallow epidermal pits, one neuromast per pit, or in grooves with variable numbers of neuromasts in single-file. Pit lines on the head consist of several short, horizontal, vertical, and transverse lines of neuromasts. The trunk in Florida Gars, for which the system is best understood, has a pair of pit lines on each side (Song & Northcutt 1991b). One line on

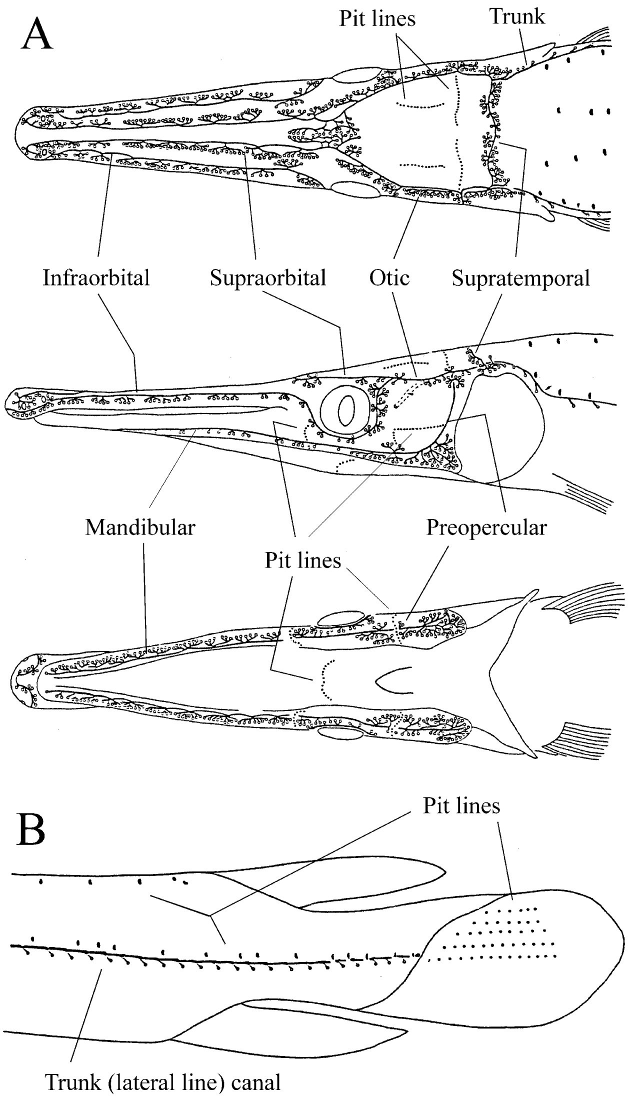

Figure 7.9. External mechanosensory canals and pit lines of the head (A) and trunk (B) in Gars. The temporal and posttemporal canals are not labeled; these connect the otic and trunk canals dorso-laterally above the operculum. The canals are tubes embedded in scales (trunk canal = lateral-line canal) or dermal plates (head) and the pit lines are linear series of epidermal depressions. The canals have short secondary tubes that terminate in pores on the surface of the fish; in the cephalic system, the secondary tubes are in groups joined by a common union with the main canal. The lateral-line canal has a single pore on each scale (used from and with permission of Song & Northcutt 1991b).

each side extends dorsolaterally from just posterior to the head to the caudal fin. The second line is on the same longitudinal scale series as the lateral-line canal. The pits begin and end with, respectively, the first and last lateral-line scales and are usually separated from neighboring pits by one or two scales. Finally, the upper half of the caudal fin has five longitudinal pit lines (Fig. 7.9B).

The sensory canal system passes through scales or dermal plates on the trunk and head, respectively. The trunk has a complete lateral-line canal with an external pore on each scale from the base of the caudal fin to the head. It is continuous with the cephalic canal system that includes a transversely oriented occipital canal, a preopercular canal, a mandibular canal, and supraorbital and infraorbital canals. The left and right supraorbital canals terminate separately near the tip of the upper jaw, but the infraorbital canals form a continuous tube around the snout tip (Fig. 7.9A, bottom). The frequency of pores in cephalic canals is much greater than in the lateral-line canal. In both systems, a single neuromast occurs between any two canal pores (Song & Northcutt 1991a).

Morphomechanics of the Jaw

The elongate bill of the living Gars is adapted to quickly snare live prey. Based on cranial measurements and lever mechanics, the jaw lever in lepisosteid Gars is one of the fastest and least forceful known for fishes (Kammerer et al. 2006). The Longnose Gar is at one extreme of speed and mechanical advantage (fastest and least forceful at the tip, respectively) and †*Masillosteus* is at the other (slowest, most forceful). The mechanical advantage of the latter, an extinct lepisosteid Gar with apparent adaptations for crushing prey, was an order of magnitude greater than that of the Longnose Gar. The other Gars fall between these extremes. The Alligator Gar has the largest opening and closing mechanical advantages among the living species. Differences in jaw mechanics are associated with food habits: shorter, wider jaws with more hard-shelled items and longer, slenderer jaws with fish eating. The interspecific differences in jaw mechanics and diets of adults are paralleled by the ontogenetic pattern in young of *Atractosteus* and *Lepisosteus*: shorter jaws with higher mechanical advantage in the early stages of exogenous feeding when the primary foods are hard-bodied microcrustaceans and longer jaws with lower mechanical advantage after the shift to a softer diet of primarily small fishes (Kammerer et al. 2006).

Lung

In respiration, Gars are bimodal, using gills for water breathing and a lung for breathing air. The lung is a highly vascularized, dorsoventrally depressed sac located above the alimentary canal. Some physiological traits indicate homology with the tetrapod lung (see physiology section), although this seems to require further investigation (Perry et al. 2001; Wilson et al. 2009). Regardless, the organs in Gars and tetrapods are sufficiently similar in form and function, including various details of physiology, that we follow Nilsson (1981) and Wilson et al. (2009) in using the term "lung" in place of the often used "air breathing organ." In Longnose Gars, the lung occupies about 10% of the volume of the fish. The lung is partitioned along its length by incomplete septa forming a number of interconnected sections that are further subdivided into many vascularized cavities (trabeculae; Rahn et al. 1971). The trabeculae have smooth and striated muscle that probably assists in buoyancy control as well as respiration (Nilsson 1981; J. B. Graham 1997).

Debate and confusion occurred about the connection between the lung and the alimentary canal in Gars (Jaroszewska & Dabrowski 2008). The questions were whether the connection is esophageal or pharyngeal, whether it involves a pneumatic duct or a common slit in the ventral wall of the lung and the dorsal wall of the alimentary canal, and whether it is muscular or not. Developmental histology of the Longnose Gar shows no connecting tube and the connection is neither muscular nor pharyngeal (Jaroszewska & Dabrowski 2008). Instead, the anterior, ventral wall of the lung directly connects to the glottis via a horizontal slit (6 mm long in a specimen 250 mm TL) in the dorsal wall of the esophagus just posterior to the pharyngeal region. The glottis is primarily composed of connective tissue that protrudes into the esophagus as a longitudinal ridge on each side of the slit. It is opened by contraction of the paired dorsal retractor muscles that extend from each pharyngeal jaw to the vertebral column and also function in the swallowing of prey. Contraction of these muscles during aerial respiration deforms the esophageal wall, causing the glottis to open (Lauder & Wainwright 1992).

Gills and Gill Surface Area

The gills of Gars follow the basic actinopterygian (Ray-finned Fishes) plan (Landolt & Hill 1975). Each of four gill arches has a pair of hemibranchs supporting the gill filaments that have numerous secondary lamellae, the sites of most gas exchange. As in many teleosts, the opposing filaments of the two hemibranchs of a gill arch are connected by a membranous interbranchial septum for almost two-thirds of the filament length. In Gars, the gill slits behind the third and fourth gill arches are progressively smaller than the first and second. The gill slit behind the fourth is so small that it likely receives little respiratory flow (Smatresk & Cameron 1982a). Like many other fishes, Gars have a small vascularized pseudobranch (false gill) on the inside wall of the operculum.

Gill surface area in Gars is small compared with that of fishes restricted to aquatic respiration (Landolt & Hill 1975; J. B. Graham 1997). The rate of increase in total gill surface area with increasing body size is slower in Gars than in a number of teleosts encompassing a wide range of activity levels from highly active tunas (Scombridae, Mackerels and Tunas; three species) to the less active roach, *Rutilus* sp. (Landolt & Hill 1975). At 1 g body weight, gill surface area is similar in roaches and Gars (4 mm^2), but at 1,000 g the roach has about twice as much (1,290 versus 660 mm^2). Another factor reducing surface area for gas exchange is the reduced and channelized, non-anastomosing circulation through the secondary lamellae as described for Spotted Gars, Shortnose Gars, and Longnose Gars (Landolt & Hill 1975; Smatresk & Cameron 1982a).

Scale Jacket

The skin in Gars generally resembles that of the Bichirs (Polypteridae), the only other extant group of ganoid fishes. These similarities include details of scale shape, organization of scales on the body, the connective tissue interconnections between scales, and the underlying connective tissue sheets (Gemballa & Bartsch 2002). Over much of the body, each scale has a dorsal peg that fits into a ventral socket of the next dorsally placed scale of the same circumferential scale row, and a short anterior process is overlapped by the adjacent scale row. The peg-and-socket structure is less pronounced in Gars than in Bichirs, and in Florida Gars, it is most pronounced laterally on the body and absent ventrally (Gemballa & Bartsch 2002).

The functional morphology of the thick, armored skin of Gars has received considerable attention. Proposed functions of ganoid scales, in addition to protection against predators, include facilitated position holding in a current because of the added weight (Webb et al. 1992), control of body stiffness and undulatory wave motion during steady swimming (Long et al. 1996), passive lung inflation (Brainerd 1994), and osmoregulation with the thick scales reducing the influx of water (Smatresk & Cameron 1982b). In body curvature, the anterior process and the peg-and-socket arrangement, where present on the body, prevent slippage overlap between dorsal and ventral margins of scales in the same circumferential (oblique) scale row, but scales of adjacent rows are allowed considerable slippage overlap. This concentrates the force of contraction and body curvature in the horizontal plane (Gemballa & Bartsch 2002).

Despite compressive rigidity, ganoid scale jackets do not necessarily restrict horizontal body curvature compared with non-ganoid fishes. The anterior body in Florida Gars, however, is less flexible than in the ganoid Bichirs (Gemballa & Bartsch 2002). This is reflected in details of the Gar scale jacket and in part might be a function of unique longitudinal tendon-like structures in the lateral parts of myosepta in the anterior portion of the body in Gars (Gemballa & Bartsch 2002). Earlier authors considered ganoid armor inferior in locomotor efficiency relative to the teleostean integument (e.g., Breder 1926), but it is more appropriately viewed as an alternative strategy with its own adaptive advantages (Long et al. 1996; Gemballa & Bartsch 2002).

GENETICS

Karyology

The karyotype is best understood for Longnose Gars and Alligator Gars. In both species the diploid chromosome number is 56, but the distribution of chromosome types differs. The Longnose Gar has 11 pairs of metacentric, 6 pairs of submetacentric, and 3 pairs of subtelocentric chromosomes, and 16 small elements called microchromosomes (Rab et al.1999). The Alligator Gar has 8 metacentric, 4 submetacentric, and 8 telocentric chromosomes, and 8 pairs of microchromosomes (Arias-Rodriguez et al. 2009). Diploid numbers are given as 68 (Ohno et al. 1969) and 54 (Ueno 1985) for the Spotted Gar. This difference might represent artifacts of technique or karyotype variation in the species. No evidence exists of sexually dimorphic chromosomes in Gars (Rab et al. 1999; Arias-Rodriguez et al. 2009).

A variety of cytological techniques in addition to standard Giemsa staining revealed details beyond gross chromosome morphology in Longnose Gars (Rab et al. 1999). Two active nucleolus-organizer regions (sites of ribosomal RNA synthesis) were detected, one at one end of each member of a pair of small metacentric macrochromosomes. The association of ribosomal DNA gene loci with GC-rich DNA apparently is a feature shared between Gars and other neopterygians (the Bowfin and teleosts) but not with Sturgeons and the Paddlefish (Rab et al. 1999).

Intraspecific Variation

An analysis of the Tropical Gar is the only molecular study of geographic variation in Gars (Barrientos & Espinosa de los Monteros 2008). This study of mtDNA sequence variation (cytochrome *b* and cytochrome oxidase subunit II) detected 23 haplotypes with a maximum sequence divergence of 2.4%. Most of the diversity (79.8% = F_{ST}*100) was attributable to differences among populations. Nested clade analysis revealed three divergent groups of populations distributed as follows: the Pacific Slope of Mesoamerica (Chiapas, Mexico, and El Salvador), the upper Rio Usumacinta drainage in Guatemala, and Gulf of Mexico–Atlantic Ocean streams including the lower Rio Usumacinta and nearby Mexican Gulf Coast streams and northeastern Costa Rica. The recent isolation and characterization of 17 polymorphic microsatellite DNA loci in the Alligator Gar provides useful tools for analyses of genetic structure in this and other Gar species (Moyer et al. 2009).

Hybridization

A number of Gar hybrids are mentioned in the pet trade, and anecdotal accounts exist of potential hybrids in the wild (Herrington et al. 2008). One pet-trade list includes combinations involving the Alligator Gar crossed with Shortnose Gars, Florida Gars, Spotted Gars, and Longnose Gars (David 2009). The only thoroughly documented Gar hybrids are 4 progeny recovered from a spontaneous spawning event in a 4,540 l tank containing 6 adult Gars, 1 Alligator Gar, 3 Longnose Gars, and 2 Spotted Gars (Herrington et al. 2008). Genetic analysis showed that a Longnose Gar was the female parent (based on mtDNA) and an Alligator Gar was the male parent. All four progeny carried the same mtDNA cytochrome *b* haplotype as one of the Longnose Gars, and they were heterozygous at two nuclear loci (tyrosinase sequence and the one microsatellite locus assayed) for alleles detected in that individual and the Alligator Gar but not in the other adult Gars in the tank.

PHYSIOLOGY

Metabolic Organization

Possibly as an adaptation to waters with low oxygen availability, most Gar tissues have a relatively low capacity for aerobic metabolism and an elevated capacity for anaerobic glycolysis (Frick et al. 2007). An exception is the lung, itself an adaptation to low aquatic oxygen, which is metabolically more similar to the mammalian lung than to the teleost swim bladder. Compared with other fishes, Gars are unusually dependent on glucose as the major fuel source (Frick et al. 2007). Plasma glucose concentrations and tissue concentrations of gluconeogenic and glycolytic enzymes in Florida Gars are elevated compared with those of the Lake Sturgeon (*Acipenser fulvescens*), the Bowfin, and several teleosts. In contrast, reliance on fatty acids as a fuel source appears lower than reported for any non-elasmobranch fish as indicated by low plasma concentrations of nonsterified (highly active metabolically) fatty acids and reduced tissue activity of enzymes responsible for lipid oxidation. Gars appear to be an exception to the rule that primitive fishes (Sea Lamprey, *Petromyzon marinus*, elasmobranchs, Lake Sturgeon) including the Bowfin, rely more heavily than teleosts on oxidation of ketone bodies as a source of energy. As in the Bowfin, but not the Lake Sturgeon and teleosts, the liver has limited capacity for fatty-acid synthesis compared with other tissues.

Blood Physiology in the Absence of a Choroid Rete

The absence in Gars of tissues (retia) specialized to generate locally low pH values is reflected in various features of blood physiology. Teleosts have a choroid rete that is absent in all other basal actinopterygians except the Bowfin (Berenbrink et al. 2005). The choroid rete, which resembles the rete mirabile in the teleostean swim bladder, is a countercurrent network of capillaries that, in association with a gas gland, maintains high oxygen concentrations in the ocular chamber of the eye, supporting the highly metabolic retina. Ocular partial pressure of oxygen in Spotted Gars and Alligator Gars is an order of magnitude smaller (90 versus 650 mm Hg) than in the Bowfin (Wittenberg & Wittenberg 1974). The release of oxygen is caused by the gas gland that metabolically (via fermentation) produces a locally high concentration of protons (H^+). The resulting pH is above the onset pH for the Root effect, a proton-induced reduction in affinity of hemoglobin for oxygen. Consequently, fish with the rete show pronounced Root effects with relatively high onset pH values, but Gars and other basal actinopterygians, except the Bowfin, do not (Regan & Brauner 2010). Spotted Gar and Alligator Gar hemoglobins have Root effect, oxygen desaturation maxima of about 10–20% at pH values of about 6.2, compared with about 30–40% desaturation at pH values of about 6.8–7.1 in the Bowfin and 2 teleosts possessing the choroid rete (Regan & Brauner 2010).

The distribution of the choroid rete in the basal lineages of neopterygians (absent in Gars, present in the Bowfin and teleosts) is interesting given the apparent sister relationship between Gars and Bowfins. Possibly, like certain aspects of osteology (see phylogenetic relationships section) the choroid rete was present in the most recent common ancestor (mrca) of Gars and Bowfins and subsequently disappeared in an ancestral Gar. Alternatively, the choroid rete might have been absent in the Gar-Bowfin mrca and appeared independently in Bowfins and teleosts. Independent losses and gains of the choroid rete or the swim bladder rete have occurred in several teleost lineages (Berenbrink et al. 2005).

Visual System

Gars have some, although limited, binocular vision (see detailed ultrastructure of the eye for Florida Gars by Collin & Collin 1993ab; Collin & Northcutt 1993, 1995). The surface of the retina facing the ocular chamber is overlain by an extensive system of blood vessels. This trait is shared with other primitive actinopterygians, presumably to satisfy retinal oxygen demand in the absence of a choroid rete. The retinal photoreceptors include rods and two types of cones. In adapting to light, the rods elongate sclerad (toward the back of the retina), narrowing in width and exposing the cones; pigment granules migrate toward the ocular chamber (vitread), blocking light from striking the rods. The reverse retinomotor events occur in adapting to the dark. The eye has a tapetum lucidum that in the dark produces a canary-yellow eyeshine when viewed with a light. Finally, the cones in Gars have spectral sensitivities and electrophysiological characteristics suggestive of the same cellular system for color vision possessed by the Bowfin, teleosts, reptiles, and mammals (Burkhardt et al. 1983). Nevertheless, no behavioral tests of Gar capacity for color vision are available.

The Lung as a Gas-exchange Organ

Potter's (1927) classical analysis of gas content in the lungs of Longnose Gars and Shortnose Gars was the first clear demonstration that some fish species could use the gas bladder as an organ of aerial gas exchange. Earlier experiments indicated that Longnose Gars could use oxygen from the air (Mark 1890), but did not show that the lung was responsible. The oxygen content of the gas in the lung was maximal immediately after a breath and then declined as carbon dioxide content increased (Potter 1927). About 50% of the gas in the lung was exchanged with each breath. The gas from disturbed fish had higher carbon dioxide content than that of resting fish. Individuals died within 4–6 h when held at low aquatic oxygen and denied access to air but not when held at higher oxygen concentrations. Plugging the glottis (or the entire lung) with paraffin also led to death.

Respiratory Control

Reflexive control via oxygen chemoreceptors plays the primary role in regulating respiratory rate in Gars, as in other fishes (Smatresk & Cameron 1982ab; Smatresk et al. 1986). Gars have two groups of oxygen receptors, one responding to the Gar's internal environment and the other responding to its external aquatic environment. With declining internal oxygen, the internal receptors increase the rate of both air breathing and gill ventilation, until at hypoxia, it loses control over the gills. When the aquatic environment is hypoxic, the external receptors switch the fish to a primarily air-breathing mode. The rate of air breathing increases as gill ventilation decreases. This increases oxygen uptake by the lung and reduces oxygen loss at the gills (Smatresk et al. 1986).

The effect of internal oxygen on gill and lung ventilation was vividly demonstrated in a preparation from Longnose Gars (Wilson et al. 2000). This preparation comprised the brainstem and the gills, opercula, and glottal region and their neuronal connections to the brainstem (cranial nerves IX and X). When the brainstem was perfused with mock cerebral spinal fluid having an oxygen partial pressure of 660 mm Hg, the gill arches moved rhythmically and the glottis was closed. With low oxygen partial pressure (67 mm Hg), gill movements ceased, and the glottis opened periodically.

Gars can adjust air breathing in response to environmental factors influencing the ecological costs of aerial versus aquatic respiration. This includes synchronous air breathing in which members of a group tend to breathe more or less in unison (Hill 1972). In addition, individuals reduce the rate of aerial breathing in the presence of a simulated aerial predator (Kramer & Graham 1976). Both of these behaviors appear to reduce the risk of aerial and aquatic predation (see subsection on behavioral regulation of air breathing).

Gars are reminiscent of tetrapods in at least two aspects of lung physiology. First, Gars seem to have an autonomous central-pattern generator in the brainstem that resembles a similar system in frog tadpoles, which like Gars, use a buccal force pump to breathe air (Wilson et al. 2000). Like tetrapods, the Longnose Gar brainstem apparently has CO_2-H^+ receptors affecting rate of lung ventilation. The isolated brainstem responds to high carbon dioxide (therefore low pH) perfusion by triggering neuronal impulses associated with increased rates of both gill and, as in tetrapods, lung ventilation (Wilson et al. 2000). Second, stretch receptors in the lung of the Spotted Gar have discharge characteristics more similar to those of Lungfishes (Ceratodontiformes) and frogs than to those of the more closely related Bowfin (Smatresk & Azizi 1987). The role of these receptors seems unclear. They might function in buoyancy regulation, rather than functioning like the mammalian Hering-Bruer reflex in controlling lung volume during respiration (Smatresk 1994).

Significance of Bimodal Respiration

Success in waters with low (hypoxic) oxygen content might have driven the evolution of aerial respiration, producing bimodal respiration (aquatic and aerial) in primitive fishes (Randall et al. 1981). Given this, the ecological and physiological significance of bimodal respiration includes a number of functions (Burleson et al. 1998): buoyancy control; avoidance of aerial predators in hypoxic water by requiring less time breathing the more oxygen-rich surface layer; support of activity and body growth in both normoxic and hypoxic water; respiratory energy efficiency in some situations (e.g., exhaustive activity) as a result of the low density and viscosity of air compared with water; and direct provision of oxygenated blood to the heart. This latter function might explain why the circulation in Gars seems inefficient in transporting oxygenated blood from the lung to the rest of the body. Oxygenated blood leaving the lung returns to the heart where it mixes with deoxygenated blood. The blood then is pumped through the gills and from there to the lung and the rest of the body. This pattern might allow direct provision of oxygenated blood from the lung to support the metabolic needs of the heart muscle itself (Brainerd 1997; Farmer 1997).

The advantage of bimodal respiration in stressful conditions is seen in a study of exercise-induced exhaustion in Spotted Gars under hypoxic (≤ 2.7 kPa P_{O2}) versus normoxic (19.3–20.7 kPa P_{O2}; non-stressful oxygen concentrations) conditions (Burleson et al. 1998). In normoxic conditions, and as a result of aerial respiration, the increase in gill ventilation with exercise was less pronounced than in unimodal water-breathing fishes. Probably because of this, Gars driven to exhaustion by exercise showed no mortality (unlike Salmonidae, Trouts and Salmons, for example). Intense aquatic ventilation is costly because of the density, viscosity, and low oxygen content/unit of water compared with air. Also, the high, exercise-induced gill-ventilation rates required to increase oxygen uptake in unimodal water breathers probably compromise other gill functions such as osmoregulation and ionic balance (Burleson et al. 1998). Gars apparently avoid such problems because of reduced gill surface area (see morphology section) and relatively minor increases in gill ventilation with exercise.

Gars in hypoxic conditions show little, if any, loss in capacity for activity. In hypoxic water, they function as unimodal air breathers because the oxygen partial pressure is greater in the blood than in the water and some oxygen is actually lost to the water (Smatresk & Cameron 1982a; Burleson et al. 1998). This loss is lower in Gars than in other fishes because of reduced gill surface area and the channelized, non-anastomosing nature of blood flow in the secondary lamellae of the gills (Smatresk & Cameron 1982a). Depressed gill ventilation in hypoxic water also reduces oxygen loss. Increased anaerobic metabolism in hypoxic water is not indicated, and the Gar lung supports a metabolic scope for activity equivalent to that supported by lungs and gills in normoxic water. This allows normal activity under conditions that "incapacitate virtually every other fish in . . . [the Gar's] environment" (Burleson et al. 1998:1367).

The Air-breathing Process

Air breathing in Gars is a four-phase buccal pump: (1) air from the lung is pulled into the buccal cavity and (2) expelled by way of the opercular slits; then (3) atmospheric air is pulled into the buccal cavity and (4) forced into the lungs (Rahn et al. 1971). The entire process requires about 1.0 s. In air breathing, the Gar approaches the water surface with the head curved slightly downward relative to the long axis of the body. A drop in the buccal floor immediately before the tip of the snout contacts the water surface draws air from the lung into the buccal cavity (Rahn et al. 1971). This flow of air might be assisted by lung compression caused by muscle fibers present (Potter 1927) in the walls of the lung trabeculae since the lung contracts when afferent nerves are electrically stimulated (Nilsson 1981). The snout breaks the surface with mouth closed; then the buccal floor lifts sharply, causing release of a large air bubble at the dorsal margin of both opercular slits. As the Gar lifts its head relative to the body and reaches its maximum vertical position (eye bisected by, corners of mouth-gape above, the water surface), the upper jaw swings open and the buccal floor drops, pulling atmospheric air into the buccal cavity. Next the mouth closes and the buccal region remains distended as the fish sinks; then the buccal floor lifts, forcing air into the lung. Finally, the mouth opens and with release of one or two small bubbles from the opercular cavity, gill ventilation resumes (Rahn et al. 1971).

Rate of Air Breathing

Gars are facultative air breathers with dependency on aerial respiration varying as a function of aquatic oxygen availability and metabolic rate. At cool temperatures, particularly when at rest, Gars rely entirely or mostly on their gills, but they switch to a combination of aquatic and aerial respiration at warm temperatures. In Spotted Gars at rest in aerated water at 19–23°C, aerial respiration accounted for only 2% (range 0–4%) of the oxygen consumed (Farmer & Jackson 1998). This changed to 53% (range 25–81%) under mild swimming conditions. In laboratory experiments rate of air breathing in both *Lepisosteus* and *Atractosteus* increases with increased water temperature (Winston 1967; De Roth 1973; Saksena 1975ab). Air-breathing rate varies negatively with oxygen partial pressure in Spotted Gars at 18°C, especially at PO_2 values of 79 mm Hg and lower (Hill et al. 1972).

Body size and rate of air breathing are positively related (Saksena 1975b). The rate of air breathing in 2 large Shortnose Gars (612–784 mm TL) was significantly higher than in 3 juveniles (251–300 mm) at each of 4 experimental temperatures (10.0, 15.5, 21.1, and 26.6°C). For example, the rate for the larger Gars at 26.6°C was nearly twice that of the juveniles (4.3–7.1 versus 0.6–3.4 breaths/h).

Air-breathing rate in Gars is affected by the daily light-dark cycles as revealed for *Lepisosteus* and *Atractosteus* in similar sets of laboratory experiments. Results suggest that the effects of light and dark are complicated by interaction with water temperature and species. The rate was consistently higher at night in Longnose Gars, Shortnose Gars, and Spotted Gars at several temperatures from 13 to 36°C (De Roth 1973; Saksena 1975ab). In juvenile Alligator Gars, however, higher rates occurred during the light phase of the day at temperatures >22.8°C (Winston 1973). Longnose Gars and Shortnose Gars showed opposite tendencies at low temperatures (2–12°C). Longnose Gars breathed more actively in the light, but Shortnose Gars continued to breathe more actively in the dark (Saksena 1975ab). The light-dark difference in breathing activity might reflect the tendency for Gars to feed more actively at night (De Roth 1973: see ecology section), but this does not explain the contrasting results for *Lepisosteus* and *Atractosteus* or the difference between Longnose Gars and Shortnose Gars at low temperatures. Experiments with 2-h light-dark cycles showed that the light-dark difference in breathing rate in Longnose Gars is a response to the presence or absence of light and not a circadian cycle entrained by diurnal periodicity (Saksena 1975a).

In the laboratory, Spotted Gars appeared to anticipate the experimental light change (sudden, not gradual) with a slight increase in breathing rate during the hour before both the onset and the offset of light (De Roth 1973). Highest breathing rates occurred, apparently as a startle response, immediately following the light changes. The difference between this response and breathing rates during the rest of the day or night was greater at 18 and 21°C than at the remaining test temperatures (13, 15, 23, and 28°C), suggesting that the greatest metabolic scope for activity is around 18 to 21°C (De Roth 1973). That is, the energy available for activity beyond routine maintenance is greater at 18–21°C than at higher or lower temperatures.

Behavioral Regulation of Air Breathing

Rate and pattern of air breathing in Gars show evidence of behavioral responses to ecological factors not directly associated with gas-exchange physiology. Like various other aquatic bimodal breathers, the members of a group of Gars sometimes show synchronous air breathing in which individuals more or less simultaneously break the water surface to breathe air (J. B. Graham 1997). This was studied in juvenile (10–17 cm TL) Longnose Gars and Spotted Gars in the laboratory (Hill 1972). The proximate basis of synchronous air breathing might be imitation in which breathing by one Gar stimulates another to breathe. Tests with heterospecific pairs (Longnose Gar and Spotted Gar) indicate that the tendency to imitate is depressed relative to homospecific pairs. There is some indication that Gars will imitate simulated breathing in a model Gar made of plaster (Hill 1972). Synchronous breathing probably functions like schooling behavior, but in a temporal rather than a spatial context, to reduce the individual Gar's risk of predation during surfacing (Kramer & Graham 1976).

In another behavioral adaptation to reduce risk of predation, individual Gars apparently alter their use of air versus water respiration when an aerial predator is detected. Florida Gars in the presence of a simulated aerial predator (a mounted Great Blue Heron) increased the time between breaths by 118% compared with the pre-heron rate, and the water-breath interval decreased by 13%. The experimental water was hypoxic (2.5 mg/l oxygen), and the test result probably would have been even more pronounced at higher oxygen levels (Smith & Kramer 1986).

Behavioral alteration of pattern and rate of air breathing probably affords protection from both aquatic and aerial predators (Kramer & Graham 1976). Surfacing and the water disturbance associated with air breathing would expose the Gar to potential predators from both above and below the water surface.

Digestion

Prolarval nutrition is entirely dependent on yolk (lecithotrophic) and some degree of lecithotrophy continues into the post-larval stage. Early post-larval Longnose Gars, Alligator Gars, and Tropical Gars use yolk in the body cavity for a time after exogenous feeding (on live prey) begins (Aguilera et al. 2002; Jaroszewska et al. 2010). Exogenous feeding begins when the larvae cease to hang from their adhesive organs. The timing varies with conditions, but it occurs in Longnose Gars at 8–10 days post-hatching (Mark 1890; Echelle & Riggs 1972) and 5 days post-hatching in Alligator Gars (Mendoza et al. 2002). A wide range of digestive enzymes (proteases, lipases, phosphatases, amylases, and pepsin) is present by the time of hatching in Alligator Gars and Cuban Gars (Mendoza et al. 2002; Comabella et al. 2006), and in both Alligator Gars and Longnose Gars, the digestive tract (e.g., stomach, pyloric caecae, and spiral fold) and associated glands and organs (e.g., liver and pancreas) are fully developed when exogenous feeding begins (Mendoza et al. 2002; Jaroszewska et al. 2010). Larval Alligator Gars and Tropical Gars reared under the same conditions were lecithotrophic when <13.5 mm TL, lecithoexotrophic between 12.5 and 22.5 mm TL, and exotrophic at >22 mm TL (Aguilera et al. 2002).

Rate of digestion in small Longnose Gars seems about twice as fast as in similarly sized Florida Gars (Hunt 1960; Netsch & Witt 1962). The fish, which averaged about 300 mm TL, were force-fed a meal of three to five small fish. Little digestion was observed after 2 h in the Longnose Gars, and no digestion occurred after 4 h in the Florida Gar. Time to complete digestion in the two species was 24 and 44–47 h, respectively. For the Florida Gar, size of meal (one, five, and nine fish) and amount of food digested/h were positively related (Hunt 1960).

Osmoregulation and Exchange of Carbon Dioxide and Ammonia

In Gars, as in fishes restricted to aquatic respiration, loss and gain of water and excretion of ammonia and carbon dioxide occur primarily by way of the gills (Smatresk & Cameron 1982c). This is true even when lung ventilation is high and gill ventilation is low, as in hypoxic water (Smatresk & Cameron 1982c). High tolerance of aquatic ammonium concentrations by Gars compared with other fishes (see pollution tolerance subsection) might reflect the ability to reduce internal levels of the most toxic form (unionized ammonia) by releasing it in volatized form during aerial exhalation (Boudreax et al. 2007b). Unlike some neopterygians, Gars retain the ancestral actinopterygian Cl^{-}-HCO_3^{-} co-transport mechanism for chloride uptake at the gills (Boudreax et al. 2007a).

Alligator Gars show considerable ability to acclimate to increasing salinity (Suchy 2009). Plasma osmolality in juveniles acclimated to increasing salinity at a rate of 1 ppt/day to several salinities between 0 and 32 ppt showed little change in plasma osmolality until salinity was >28 ppt, but increasing plasma osmolality began at 12 ppt in non-acclimated fish. Similar experiments with juvenile Spotted Gars indicated less ability to accommodate high salinities. Plasma osmolality in acclimated fish steadily increased at salinities ranging from 9 to 32 ppt. A similar pattern occurred in non-acclimated Spotted Gars except that all fish died at salinities >16 ppt.

Urinary flow rate in Spotted Gars is low for a freshwater fish (Smatresk & Cameron 1982bc). This probably reflects reduced influx of water as a result of the Gar's reduced gill surface area, as well as the thick ganoid armor that probably retards water influx (Smatresk & Cameron 1982b). When transferred from fresh water to 50% sea water at 26°C, blood osmolarity of Spotted Gars increased sharply during the first 24 h and then returned to the previous level by 5 days after the transfer. Acidosis induced by the transfer did not diminish during those 5 days (Smatresk & Cameron 1982b).

Exercise-induced exhaustion causes a marked acidosis in Spotted Gars that persists several times longer than in other, similarly treated fishes, but Gars seem more tolerant of acidosis than other fishes (Burleson et al. 1998). Acidosis induced by hypoxia or exposure to sea water is not an effect of heightened anaerobic metabolism; instead it reflects the Gar's reduced carbon dioxide exchange as a result of reduced gill ventilation (Smatresk & Cameron 1982b; Burleson et al. 1998). Despite elevated lung ventilation and reduced gill ventilation during hypoxia, the gills still represent the primary site of carbon dioxide exchange, and therefore, overall acid-base balance of the fish (Smatresk & Cameron 1982b).

Salinity Tolerance

Although Gars inhabit primarily fresh water, some species occasionally occur in brackish water, and Alligator Gars sometimes occur in full or near-full strength sea water (Gunter 1945; Suttkus 1963). The maximum salinity of capture in a survey of the Mississippi Gulf Coast was 25 ppt for Alligator Gars and 15 ppt for Longnose Gars and Spotted Gars (Goodyear 1966). In Virginia, Longnose Gars occurred at a salinity of 21 ppt (McGrath 2010).

Tolerance of Alligator Gars to elevated salinities increases with age and developmental stage (Suchy 2009). Laboratory tests indicate that the prolarvae cannot survive salinities >8 ppt. Significant mortality and reduced growth occurred at 8 ppt, and no survival occurred at 10, 12, and 14 ppt. All larvae survived at 0, 2, 4, and 6 ppt with no differences in growth rate. Early juveniles (20 days post-hatching) survived at 12 ppt with stepwise acclimation to the end of the study 31 days later, but growth was slower and mortality was higher than at 4 and 8 ppt. Juveniles at 50 days post-hatching showed no difference in mortality and little difference in growth at salinities of 0, 6, 12, and 18 ppt.

Juvenile Alligator Gars and Spotted Gars are tolerant of higher salinities than are juvenile Paddlefish and Lake Sturgeons (Suchy 2009). Non-acclimated Paddlefish and Lake Sturgeons showed 100% mortality at 16 ppt, but Spotted Gars and Alligator Gars did not reach 100% mortality until 20 ppt and 36 ppt, respectively. The Paddlefish and Lake Sturgeon showed no improvement with acclimation, but with acclimation, juvenile Spotted Gars (average TL 122 mm) and Alligator Gars (199 mm TL) tolerated salinities ≤30 and 37 ppt, respectively. Florida Gars apparently resemble Spotted Gars in salinity tolerance; juveniles tolerated 75% sea water (about 26 ppt) during a 2-week acclimation period before osmoregulation experiments, but they were unable to tolerate full-strength sea water (about 35 ppt; Zawodny 1975).

pH Tolerance

Gars appear to be relatively tolerant of acidic waters compared with other fishes. Survival time was not affected in juvenile Florida Gars exposed to pH as low as 3.8, but at 3.6 there was a significant effect with an average survival time of about 40 h (Krout & Dunson 1985). Death at low pH was associated with a large increase in net sodium loss, suggesting that the cause of death involves ionic imbalance. Tolerance to low pH was correlated with a high capacity for resisting the net sodium loss usually associated with pH toxicity in fishes.

Pollution Tolerance

Air breathing apparently makes Gars more tolerant of pollutants affecting uptake of oxygen at the gills. For example, in 1988, an estimated 37,000 fishes died in a series of fish-kills in the Fox River, Wisconsin, from carbon monoxide pollution produced by motorboat engines. Gars were present in the river but were not included in the kills (Kempinger et al. 1998).

On the other hand, Gars are undoubtedly adversely affected by many aquatic pollutants. As long-lived top predators, they are susceptible to bioaccumulating compounds such as organophosphate pesticides and heavy metals (Cruz et al. 2010). Spotted Gars from a petroleum-contaminated site in Louisiana showed gonadal cysts in both sexes (4 of 30 males; 1 of 42 females). The sample from the control site was relatively small (17 males, 15 females), but no cysts were detected (Thiyagarajah et al. 2000).

Gars seem to have relatively high tolerance to dissolved ammonium concentrations. This is particularly true of Alligator Gars, which in a recent review had the highest tolerance known for fishes (Boudreax et al. 2007b). The Spotted Gar had greater tolerance than all except 2 of 12 non-Gar species included in the review. The exceptions were relatively hardy species (Common Carp, *Cyprinus carpio*, and Red Shiner, *Cyprinella lutrensis*). The 96-h median-lethal concentrations for total ammonia and unionized ammonia were 135 and 4.30 ppm, respectively, for Alligator Gars. The corresponding values for Spotted Gars were 35 and 1.82 ppm. High ammonia tolerance in Gars might be explained as an adaptation to their high-protein, therefore high-nitrogen diets (Boudreax et al. 2007b).

Gars tend to concentrate aquatic nitrite internally (Boudreax et al. 2007a). This is because they retain the ancestral actinopterygian mechanism for chloride uptake (see osmoregulation and exchange of carbon dioxide and ammonia subsection) and nitrite competes with chloride for this mechanism of transport across the gill membranes. Because of this competitive relationship, tolerance to nitrite pollution is higher in waters containing higher chloride content. Gars exposed to 1 ppm nitrite and 20 ppm chloride survived better than those exposed to 1 ppm nitrite and <1 ppm chloride. Heightened chloride concentration effectively prevented nitrite concentration in the plasma.

Dissolved Oxygen Tolerance

Gars with access to air are relatively insensitive to the oxygen content of the water (Renfro & Hill 1970). Spotted Gars tolerate water at near zero oxygen content at temperatures as high as 30°C (Hill et al. 1972). Florida Gars denied access to air died within 1 h at 2.5 mg/l oxygen and 20°C (McCormack 1967). Spotted Gars with access to air and at 3 different temperatures (10, 21, and 30°C) behaved more or less independently of aquatic oxygen when given the choice between an acclimation oxygen level (3.6 mg/l) and test concentrations from <1 to 21 mg/l (Hill et al. 1973). When denied access to air, they consistently avoided oxygen levels lower than the acclimation level of 3.6 mg/l and preferred intermediate (6–11 mg/l) over high to extremely high (12–21 mg/l) concentrations. The preference for intermediate oxygen levels was especially pronounced at the highest temperature tested (30°C).

Thermoregulation

Gars in warm water are required to remain near the surface for aerial respiration. Thus, unlike most fishes, they are not as free to seek refuge in deeper, cooler water. Possibly for this reason, Gars had higher body temperatures (average, 31°C) than 11 other fishes in an area of a lake receiving heated effluent from a power plant (Neill & Magnuson 1974).

Gar Toxicity

The potential toxicity of Gar eggs has been known since 1851 when a medical doctor reported that after a family of five had eaten Gar, including eggs, they suffered "a burning sensation in the pit of the stomach, which was soon succeeded by vomiting, purging, and cramping, in their most aggravated form" (W. Brooks, quoted from Broussard 2009:4). Now it is well established that the oocytes, eggs, and early larvae are toxic (Broussard 2009). The toxin is destroyed after 10 min of boiling and appears to be a small-molecule (3,000 Daltons), probably proteinaceous substance (Broussard 2009). Some toxicity was detected in the blood, and it is present in non-vitellogenic oocytes. Oocyte toxicity reaches maximal potency with the onset of vitellogenesis and remains high until the eggs are released at spawning. Potency declines as the larvae age, but measureable toxicity remains as late as 15 days after hatching.

Animals known to be susceptible to Gar toxin include humans, mice, and chickens (Netsch & Witt 1962) and a variety of crustaceans, including crayfishes, grass shrimp, and crabs (Burns et al. 1981; Broussard 2009). Dogs, cats, mice, and chickens apparently resist eating the eggs unless starved (Netsch & Witt 1962). Mice force-fed 0.2 ml of egg homogenate became sick within 18 h and recovery took ≤2 days (Netsch & Witt 1962). All tested crustaceans died when injected with 4 μl of supernatant from a homogenate of 5 g of Gar eggs in 20 ml of a saline solution (Broussard 2009).

Animals that appear unaffected by Gar toxin include a species of cricket and a taxonomically diverse group of aquatic or semi-aquatic animals. These include a snail, a treefrog, a turtle, the Paddlefish, two species of Sunfishes (Centrarchidae), a Killifish (Fundulidae), two Livebearers (Poeciliidae), a North American Catfish (Ictaluridae), and a Sucker (Catostomidae) (Netsch & Witt 1962; Goodger & Burns 1980; Ostrand et al. 1996; Broussard 2009). The Green Sunfish (*Lepomis cyanellus*) and Channel Catfish (*Ictalurus punctatus*) feed readily on Alligator Gar eggs without suffering (Burns et al. 1981), and Gar eggs occurred in the stomachs of Bluegills (*Lepomis macrochirus*) and River Carpsuckers (*Carpiodes carpio*) that appeared to have suffered no ill effects (Netsch & Witt 1962).

The physiological mechanism of Gar toxicity seems related to interference with Ca^{++} transport by cell membranes. A neurotoxic effect apparently caused by interference with Ca^{++} transport was detected in a crayfish neuromuscular preparation (Broussard 2009). Intact Red-eared Sliders (*Trachemys scripta*) were unaffected by injection with Gar toxin, but a heart preparation showed cardiac arrest when perfused with 8.8 mg/ml of Alligator Gar egg protein (Goodger & Burns 1980). Characteristics of the heart response suggested that the toxin interfered with Ca^{++} transport.

BEHAVIOR

Prolarvae

The prolarvae (yolk-sac larvae; Hubbs 1943), although capable of vigorous undulatory (anguilliform) swimming, are relatively inactive and spend most of their time hanging from objects off or on the bottom near the site of egg deposition (Echelle & Riggs 1972; Inebnit 2009). There is no behavioral tendency to aggregate, but they can be locally abundant in the spawning habitat. The prolarvae are denser than water and sink toward the bottom unless they start swimming. In attaching to an object, the larva swims to it and briefly continues undulating, causing the snout to swing from side to side against the surface; then movement ceases and the larva hangs suspended by its adhesive organ (Echelle 1967). Objects for attachment can be vegetation, floating twigs, the bottom substratum, or other surfaces, including the surface film of the water (Agassiz 1879; Mark 1890; Goff 1984). In a situation where large numbers of Alligator Gar prolarvae were hanging from submerged vegetation, agitated individuals would swim "to the next available attachment site," including the surface film (Inebnit 2009:17).

Post-Larvae

Soon after yolk sac absorption, larvae cease to hang vertically and can rest horizontally in the water column, which they often do in the vicinity of floating leaves or twigs. They may continue to attach to objects with the adhesive organ for a brief period, but they remain horizontal. By this time in aquaria they take their first aerial breath, become more active, and begin to feed on living prey (Echelle & Riggs 1972). As in adults, the feeding strike involves a lateral swipe of the head (Comabella et al. 2010). There is no tendency for schooling behavior.

Pre-Juveniles

Little is known about movement in pre-juveniles. At night, young Gars are often seen swimming actively, but during the day they usually rest more or less motionlessly in close association with submerged or overhanging objects near shore (Echelle & Riggs 1972). One Longnose Gar apparently spent the daylight hours beneath the same overhanging limb from mid-July to 1 September when it was captured and measured at 305 mm TL.

The caudal filament (see morphology section) characteristic of pre-juveniles is used, along with the pectoral fins, to produce slow, "almost imperceptible" stalking of live prey (Carpenter 1975:59). The tip alone or, for more force, a larger portion of the filament, vibrates laterally (flutters) at rates of up to 15–16 beats/s but usually at 3–8 beats/s. The individual beat is a wave that passes distally to the tip of the filament. In forward movement, the fluttering filament extends straight backward with the pectoral fins (beating at a similar rate) projecting down and slightly posterior. In backward movement, the filament curves laterally and somewhat down to either side with the tip pointing slightly forward; the pectorals project down and forward. In straight backward movement and slow backward turning, the caudal fin is motionless and extends straight back. In rapid backward turns the caudal fin bends more or less in the same plane as the caudal filament and may or may not make a waving motion. By altering the angle of the filament, the fish can slowly tilt the body head up or head down (Carpenter 1975).

Adult Locomotion

Adult Gars generally are non-schooling, relatively sluggish fish. They often lurk individually near the water surface, maintaining position with fin movements and occasionally breaking the surface to breathe air. They are capable of rapid fast-start swimming, but the fast-start velocity is lower than that of the less heavily scaled, similarly shaped Tiger Musky (Northern Pike, *Esox lucius* × Muskellunge, *E. masquinongy*), reflecting a tradeoff between skin mass and muscle mass (Webb et al. 1992).

Steady swimming in adult Gars is accomplished by waves of undulation involving only the posterior third of the body with the rest of the body held rigid (Gemballa & Bartsch 2002). The wave amplitude at the end of the body is about 10% of body length. Extreme turns also involve bending in only the posterior third of the body. This is not a limitation necessarily imposed by ganoid armor because in fast starts (Gemballa & Bartsch 2002) and in preparing to deliver a feeding strike (Porter & Motta 2004) both the anterior and the posterior halves of the body can be involved in body curvature.

Home Range and Movements

Telemetry (radio or sonic) was used to quantify movements and habitat use of Spotted Gars (Snedden et al. 1999), Alligator Gars (Sakaris et al. 2003; Brinkman 2008), and Longnose Gars (McGrath 2010). Movements of Spotted Gars in the Atchafalaya Basin, Louisiana, were monitored on a diel (27 fish) and a seasonal (37 fish) basis during a 2-year period (Snedden et al. 1999). Hourly movement, which ranged from 0.0 to 839 m/h (median 22 m/h), was greater in summer than in autumn-winter, and in both periods, activity was significantly greater at night than during the day. Daily movement ranged from 0 to 1,837 m/day (median 58 m/day), and the rate was greater in the spring (130 m/day) than in summer (36 m/day) or autumn–winter (35 m/day). Home range was smaller in the summer and autumn-winter (1–78 ha; median 7 ha); the marked Gars typically stayed ≤2 km of the initial capture site. In contrast, 19 Gars marked at one locality in February remained in the local area until March, when following a rise in water level, they dispersed out of the local area. Thirteen were found by aerial telemetry, 9 of which had moved to another area 4 km away. Four individuals occupied more than one home range during the springtime rise in water levels. After several weeks in one area they moved to another, where they stayed for extended periods.

A 13-month study of movements in 6 Alligator Gars in streams of the Mobile-Tensaw Delta, Alabama (Sakaris et al. 2003), showed a significant positive relationship between body size and distance moved between telemetric relocation of individuals. The association between linear home range and body size was not significant, but the home ranges of the smallest (970 mm TL) and the largest (1,935 mm TL) individuals did represent the range of values for the study (3–12 km; mean 7 km). A similar, 9-month study of Alligator Gars in a shallow arm of Lake Texoma (Brinkman 2008) found somewhat larger linear home ranges (mean 15 km; range 6–50 km; n = 6). All except one of these fish were hatchery brood stock fish that were tracked after repatriation into the lake. There was no significant effect of body size. The one wild-caught fish was the largest (1,970 mm TL) of the study, and it had the highest average daily distance moved (1.6 km) and the largest linear home range (50 km). The 5 other fish (1,154–1,595 mm TL) had linear home ranges of 6–12 km. Home range area ranged from 5 to 17 km^2 for the Oklahoma fish. Home ranges of the Alabama stream population were essentially one-dimensional.

Longnose Gars might show greater amplitudes of movement than other Gars. A 1-year study of sonically tagged Longnose Gars in tidal streams of Virginia had a high frequency of fish (8 of 17) that were relocated only once or twice before apparently moving out of the range of detection (McGrath 2010). Five tagged fish (801–1,110 mm TL) survived to the end of the study and were relocated on ≥3 days. Time between release and last detection was 35–396 days (mean 183 days), and average distance traveled was 31 km (range <1–74.0 km). Two long-distance movements involved Gars that moved minimum distances of 69 and 74 km during several months between tagging and the first relocation. Both fish had changed rivers of occupancy and established home ranges where they remained for several months before the transmitters failed. An instance of relatively long-distance movement in Missouri involved a post-spawning individual that was found 48 km away from its spawning grounds where it had been marked with visible tags about 5 months earlier (Johnson & Noltie 1997).

At warm temperatures, Gars are obligated to live in the shallows or near the surface in deep waters, and they appear to show no tendency to aggregate. In the winter, however, Longnose Gars in the Kansas River congregate at the bottoms of deep pools (Cross 1967). Mixed winter-time congregations of Longnose Gars, Shortnose Gars, and Alligator Gars occurred repeatedly at one site in a relatively shallow arm of Lake Texoma (Brinkman 2008). These congregations formed when mid-depth temperatures were <12°C, and they dispersed at warmer temperatures. The site was about 6 m deep and seemed indistinguishable from similar spots in the area. Gars were using the entire water column and occasionally surfaced to breathe air.

Feeding Behavior

Gars are often described as lie-in-wait predators or slow stalkers that might follow prey for several minutes (Pflieger 1997; Porter & Motta 2004). But they also will patrol actively for food, as, for example, in a situation in Missouri where Shortnose Gars were patrolling the water surface for dying cicadas caught in the stream flow during an emergence of 13- and 17-year periodic cicadas (Vokoun 2000). Similarly, during incoming or high tides in bayous near the Mississippi Gulf Coast, Spotted Gars moved from deep waters to the shallower edges, where they patrolled in search of small crabs (Goodyear 1967).

The Gar feeding act involves three phases: an initial strike, prey manipulation, and swallowing (detailed by Lauder 1980; Lauder & Norton 1980). Prey capture involves a unique striking behavior (Lauder 1980; Porter & Motta 2004). The Gar first aligns its head laterally to the prey, bends the body laterally in an S-shape, head and anterior body concave toward the prey and posterior body and caudal fin convex. Then, with a sidewise swipe of the head, the jaws open (assisted by a lifting of the neurocranium) and then close on the prey, impaling it on the sharp teeth, usually with the prey perpendicular to the jaws (Fig. 7.10). With quick lateral movements of the head and short forward lunges, the Gar manipulates the prey toward the buccal cavity and finally transports it into the buccal cavity by suction.

Prey manipulation after capture involves two different patterns (Lauder & Norton 1980). In Type I the head swings laterally, the mouth opens, and the jaws close on the prey nearer to the head than it was before. In Type II manipulation, the prey is rotated from its original perpendicular position relative to the jaws to a more parallel orientation before entering the buccal cavity. Attempts to swallow a fish tail-first usually result in its ejection from the buccal cavity and another round of manipulation. The sidewise swipe is short and extremely rapid, requiring only 25–45 ms in Florida Gars and Spotted Gars (Lauder 1980; Porter and Motta 2004).

Agonistic Behavior and Feeding Territoriality

The only reported instance of territoriality in Gars was described for the aforementioned instance of Shortnose Gars feeding on periodic cicadas (Vokoun 2000). In different pools of this stream, the largest Gar occupied the upstream edge of the pool, where it had a feeding advantage because it had the first chance to feed on cicadas drifting into the pool from upstream. A pool chosen for tests contained one large Gar (550 mm TL) and two groups of smaller Gars (450–475 and 375–400 mm). The largest Gar stayed near the upstream lip of the pool and the two smaller groups were segregated with the mid-sized and small-sized Gars nearer the head and the tail of the pool, respectively. Experiments indicated a dominance hierarchy based on feeding-site favorability. The spatial arrangement tended to break down when a surplus of cicadas was provided artificially, largely because of post-capture manipulation of the cicada by the largest Gar, when it tended to drift out of its territory.

Overt agonistic behavior in the cicada-feeding Gar occurred only when the number of floating cicadas entering the pool from upstream was artificially increased (Vokoun 2000). Then the largest Gar repeatedly defended the

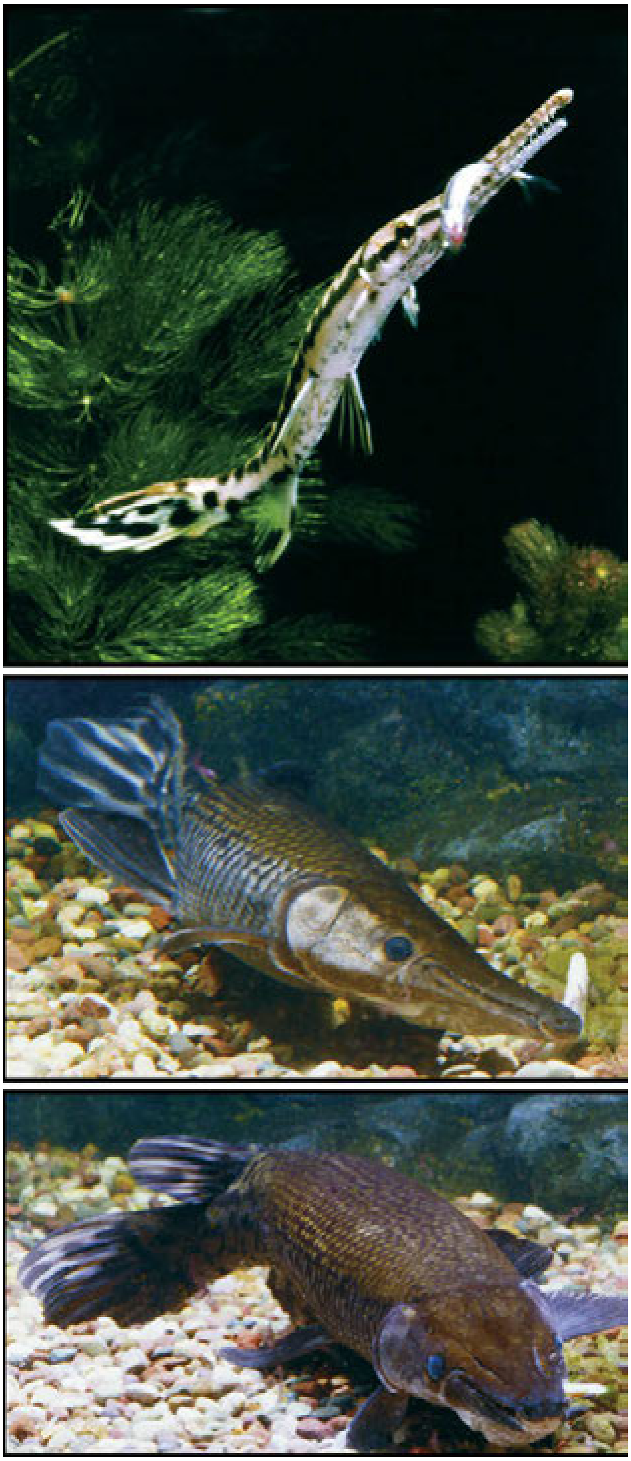

Figure 7.10. Different feeding strategies in Gars. *Top*: Longnose Gar, *Lepisosteus osseus*; young aquarium specimen about 250 mm TL grabbing a food fish out of the upper water column. This individual still retains the dark brown band along the side of the body characteristic of young individuals (photograph by and used with permission of P. Ceisel). *Middle and bottom*: Alligator Gar, *Atractosteus spatula*; aquarium specimen about 780 mm TL grabbing a dead fish off the bottom with its broad, thick bill and stout teeth (used from Grande 2010 with permission of the American Society of Ichthyologists and Herpetologists).

upstream area of the pool, whether a cicada was present or not. Defense consisted of chasing or a previously undescribed behavior that occurred in response to slowly approaching intruders. In this behavior, the largest Gar oriented perpendicularly to such an intruder and drifted downstream toward it. This usually caused the intruder to leave, but, if it persisted until its snout made contact with the aggressor, the latter would turn, snap at the intruder's body, and chase it downstream. On the other hand, the largest Gar did not pursue cicadas downstream into areas occupied by the smaller individuals.

REPRODUCTION

Age at Maturation

Estimates of age at maturation often differ between studies of the same species. For Spotted Gars in Lake Pontchartrain, Louisiana, both sexes reached maturity within the first 2 years of life (Love 2004), but Ferrara (2001), without mentioning males, estimated that females in a Georgia population were not mature until age 4. The estimates for a Missouri population were ages 2–3 for males and ages 3–4 for females (Redmond 1964). Results for Longnose Gars are fairly consistent over a wide area of the eastern United States; males reach maturity at ages 2–4 and females at ages 6–7 (Netsch & Witt 1962; Haase 1969; Ferrara 2001; McGrath 2010). The estimates for Alligator Gars in the southeastern United States were 6 years for males and 10–14 years for females (Ferrara 2001). Those estimates differ widely from DiBenedetto's (2009) estimates of 4 and 5 years, respectively, for a population in Louisiana.

Sexual Dimorphism

Gars show little easily noted sexual dimorphism except that adult females are larger than males (Suttkus 1963). After removing age effects, female Spotted Gars have longer bodies and longer snouts than males, but body mass and depth and snout width are not sexually dimorphic (Love 2002).

Seasonality

In North America, Gars usually begin to spawn in the spring when photoperiod is increasing and temperatures and water levels are rising. Most estimates of spawning seasonality in Gars are from observations of breeding activity or from measures of gonadal condition, usually the wet-weight gonad somatic index (GSI; gonadal weight / body weight).

A multifaceted approach to understanding reproductive seasonality in male and female Florida Gars was based on GSI, together with histology of the gonads and plasma concentrations of several hormones related to reproduction (Orlando et al. 2003, 2007). In both sexes, a gonadally quiescent late spring and summer period (April–September) was followed by increased gonadal activity in autumn and winter. Maximal GSI in females occurred in February, along with the first evidence of ovulation. This was followed in March by a sharp decline in female GSI. Most females spawned in February and March, after which the various reproductive parameters declined to basal levels in both males and females. The ovaries showed two waves of oocyte development, suggesting that, although not observed, some spawning might have occurred subsequent to the February–March spawning period.

A shift toward later spawning seasons at higher latitudes is indicated by the following seasons (arranged south to north): February–March into May for Spotted Gars (Love 2004; Smith 2008) and Alligator Gars (DiBenedetto 2009) in Louisiana; early to mid-April to early June for a population of Longnose Gars and two populations of Spotted Gars in Oklahoma (Echelle & Riggs 1972; Tyler & Granger 1984); late April into June for Longnose Gars and Spotted Gars in Missouri (Johnson & Noltie 1996) and Longnose Gars in Virginia (McGrath 2010); and May and June for Shortnose Gars in Wisconsin and South Dakota (Becker 1983) and Longnose Gars in Wisconsin (Haase 1969; Becker 1983) and New York (Dean 1895).

Species of *Atractosteus* in Mexico and Costa Rica seem to delay spawning until at least the beginning of the wet season in May and April, respectively. Alligator Gars in Vicente Guerrero Reservoir, Tamaulipas, Mexico, spawn as early as May and as late as September with maximum activity in August (Garcia de León et al. 2001). Tropical Gars in Tabasco, Mexico, reportedly spawn in August and September at the height of the wet season (Reséndez & Salvadores 1983). In Costa Rica, Tropical Gars begin spawning in April at the beginning of the wet season and spawning occurs as late as the end of the wet season in October (Mora et al. 1997).

Spawning Movements

Spawning in Gars generally is associated with movement into shallow waters with little evidence of long-distance migration. For example, Alligator Gars make seasonal movements into the littoral zones of lakes (Garcia de León et al. 2001), inundated bottomland forest (Suttkus 1963), and recently inundated areas of shoreline vegetation (Brinkman 2008). In Deer Lake, Atchafalaya Basin, Louisiana, Spotted Gars move onto the inundated floodplain to feed and spawn (Snedden et al. 1999). Spawning aggregations of Longnose Gars occurred in shallow waters of Lake Mendota, Wisconsin (Haase 1969), and at the edge of a river in Virginia (McGrath 2010).

Various authors have suggested anecdotally that river- and lake-dwelling Longnose Gars move upstream in rivers or into smaller tributaries for spawning (Cross 1967; Johnson & Noltie 1996). For example, Netsch and Witt (1962:259) suggested that Longnose Gars in Missouri "probably move upstream to spawn coincident with spring freshets." Upstream migration is not a requisite for spawning because the species commonly spawns in lakes (see spawning behavior subsection).

The best evidence for spawning migration in Gars is from a study of a Longnose Gar population in Harry S. Truman Reservoir, Missouri (Johnson & Noltie 1996). From early April to late May, individuals moved from the reservoir ≤10 km upstream in Weaubleau Creek, where they were absent for most of the year. Migration into the creek increased with increasing temperature and stream flow and declined with decreasing temperature. Residence time of individuals ranged from 15 to 94 days and averaged 34 days for females and 49 days for males. Remnant individuals from the migration remained into July.

The degree of spawning-site fidelity in individual Gars is unknown. For the population in Harry S. Truman Reservoir, 12.6% (3 of 24) of the spawning migrants marked in Weaubleau Creek in 1991 returned with the 1992 spawning migration. This might represent some degree of site fidelity, but the study was not designed to test whether the returns were more frequent than expected by chance (Johnson & Noltie 1996).

Spawning Habitat and Cues

Longnose Gars in lacustrine situations often spawn on relatively barren, rocky points and open shorelines (Fig. 7.11), and eggs once were found attached to gravel in the nests of the Smallmouth Bass, *Micropterus dolomieu* (Goff 1984). Spawning in other Gars usually occurs in quiet-water, vegetated habitats such as swamps, bayous, shallow bays, inundated floodplains of lakes and rivers, and stream pools and backwaters (Fig. 7.11). Eggs are generally found attached to submerged vegetation or the bottom substrate.

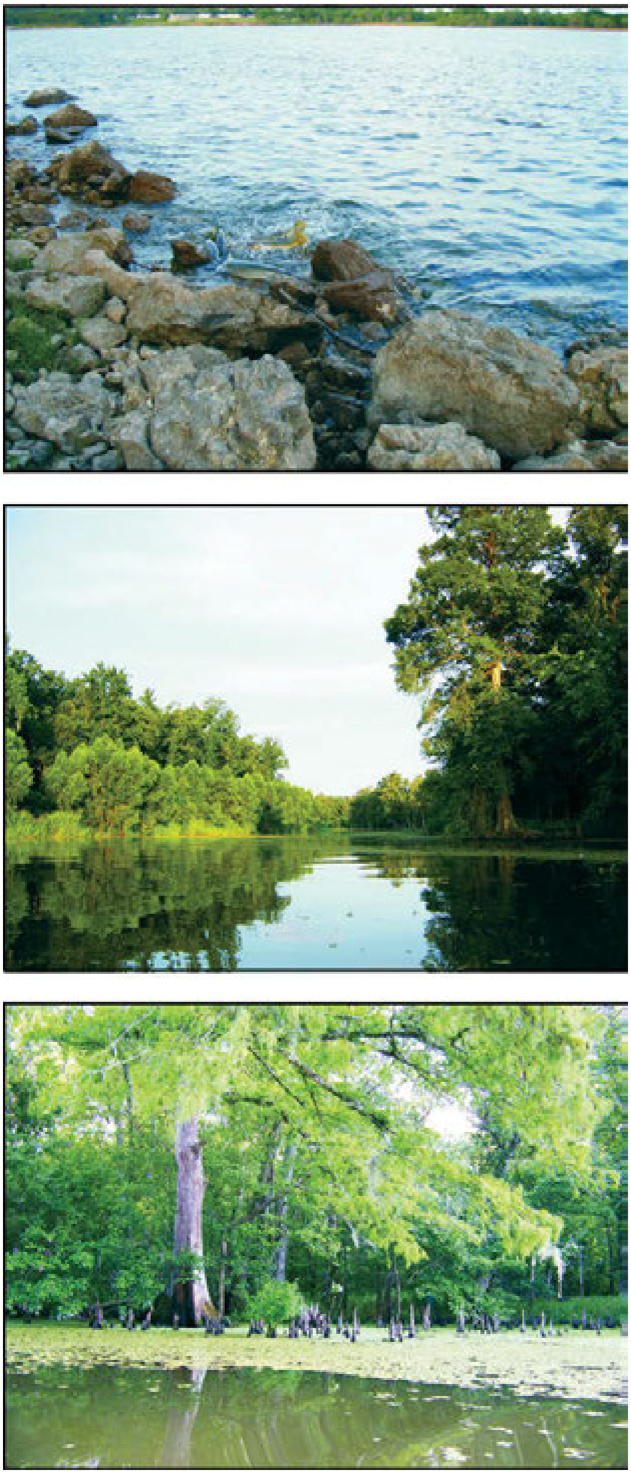

Figure 7.11. Top: Example of spawning habitat for Longnose Gar, *Lepisosteus osseus*, in Lake Texoma, Oklahoma (note spawning group left of center, large female out of water). *Middle and bottom*: Habitats occupied by Spotted Gar, *Lepisosteus oculatus*, and Alligator Gar, *Atractosteus spatula*, in Bayou Chevreuil, St. James Parish, Louisiana (photographs by and used with permission of C. Vaughn, *top*, and A. Ferrara, *middle and bottom*).

Minimum temperatures undoubtedly exist for spawning in Gars, and a variety of studies indicate that spawning may be associated with rising waters. In Longnose Gars in Lake Mendota, Wisconsin, the "immediate stimulus for the formation of spawning groups" seemed to be rising water temperatures (Haase 1969:193). Spawning occurred at temperatures from 15 to 24°C with peaks at 20–21°C. Similarly, in a New York population of Longnose Gars, spawning occurred at temperatures of 20–21°C (Agassiz 1879). The minimum temperature for Longnose Gars spawning in Weaubleau Creek, Missouri, "may approximate" 16.5°C (Johnson & Noltie 1996:102). In that situation, migration into Weaubleau Creek for spawning was positively correlated with water flow associated with rain events during the spawning season (Johnson & Noltie 1996).

At more southern latitudes (Oklahoma, Arkansas, and Louisiana), Spotted Gars and Alligator Gars move into and spawn in recently flooded wetlands and backwater habitat (Pigg & Gibbs 1996; Snedden et al. 1999; Brinkman 2008; Inebnit 2009). Spawning in Alligator Gars was observed at water temperatures of 27.5–29.5°C in Arkansas (Inebnit 2009). In Costa Rica, Tropical Gars apparently move out of the river channels into shallow lakes that form at the beginning of the wet season (Bussing 1998; Mora et al. 1997). Similarly, Alligator Gars in northeastern Mexico initiate spawning at the beginning of the wet season (Garcia de León et al. 2001). Such observations suggest that in persistently warm regions rising waters or associated conditions might be more important than temperature as cues for spawning activity.

Spawning is most commonly reported as occurring in daylight hours, although Longnose Gars occasionally spawn at night (Haase 1969). There are reports of Alligator Gars and Tropical Gars spawning at night in Mexico (Mendoza et al. 2010a).

Spawning Behavior

Breeding behavior in Gars seems similar across the species and is described for Longnose Gars (Dean 1895; Haase 1969), Alligator Gars (Brinkman 2008; Inebnit 2009), and Spotted Gars (Echelle 1967; Love 2004). The most detailed description is Haase's (1969:86–87) report for the Longnose Gar. After attracting one to several males, a receptive female leads them around in an elliptical path for ≤15 min before spawning (Fig. 7.12). The males form a tight group around the female and with sidewise movements of the snout nudge her laterally or ventro-laterally in the pectoral region or farther back. To spawn, the group positions itself at one place with their bodies somewhat tilted head downward, snouts almost touching the substrate and males continuing to nudge the female. Then follows a "rapid, violent quivering" with dispersal of eggs and sperm and some forward movement of the group, after which another round of leading and spawning might occur. One particular female spawned "up to six times in a 15-min period and 27 times in three hours." The sex ratio in the spawning area was skewed toward males and at times no females were present.

Longnose Gars often spawn in relatively open-water situations (Fig. 7.11). Spawning occurred along rocky shorelines and over points that were the extremities of small capes extending out into a lake (Agassiz 1879; Mark 1890; Matthews et al. 2012). In Lake Mendota, Wisconsin, spawning occurred in a variety of shoreline areas where the only vegetation was filamentous algae (*Cladophora* sp.) and the substrate varied from boulders, rock-rubble, and rocky shelves to a gravel bed (Haase 1969). Rocky substrate is not necessarily required for spawning because in Lake Texoma, Oklahoma, a group spawned 11 times over a 45-min period in a stump-filled area at the mouth of a bay (Echelle 1967).

Spawning behavior in other Gars seems similar to that of Longnose Gars except that it usually is described from more heavily vegetated habitats. For example, a spawning aggregation of about 50 Alligator Gars occurred in a shallow (<0.3 m) backwater area of recently flooded spike rush (*Eleocharis* sp.) in Lake Texoma (Brinkman 2008). Spawning occurred in groups of 4 to 12 individuals consisting of 1 large (≥1.8 m TL), presumably female, Gar and several smaller Gars, presumably males. In two separate years Alligator Gars spawned in the same tributary backwater of the Fourche LaFave River, Arkansas (Inebnit 2009). A group of two to four Gars made repeated spawning passes in a series of spawning events lasting 3.5 h. After spawning, the group swam into deeper water and eventually returned to spawn again. Apparently only one female was involved because no more than one spawning bout was occurring at a given time (Inebnit 2009).

Spotted Gars in Lake Texoma, Oklahoma, spawned in groups of two to four fish in shallow water (<0.3 m) with abundant submergent vegetation (Echelle 1967). Before spawning the female meandered about, often with a male on each side. The males seemed to be trying to keep their snouts touching the underside of the female's venter at, or just posterior to the area of her pectoral fins. At times a male strayed away briefly, and occasionally one to three males trailed just behind the female. The female initiated spawning by stopping her forward movement and making

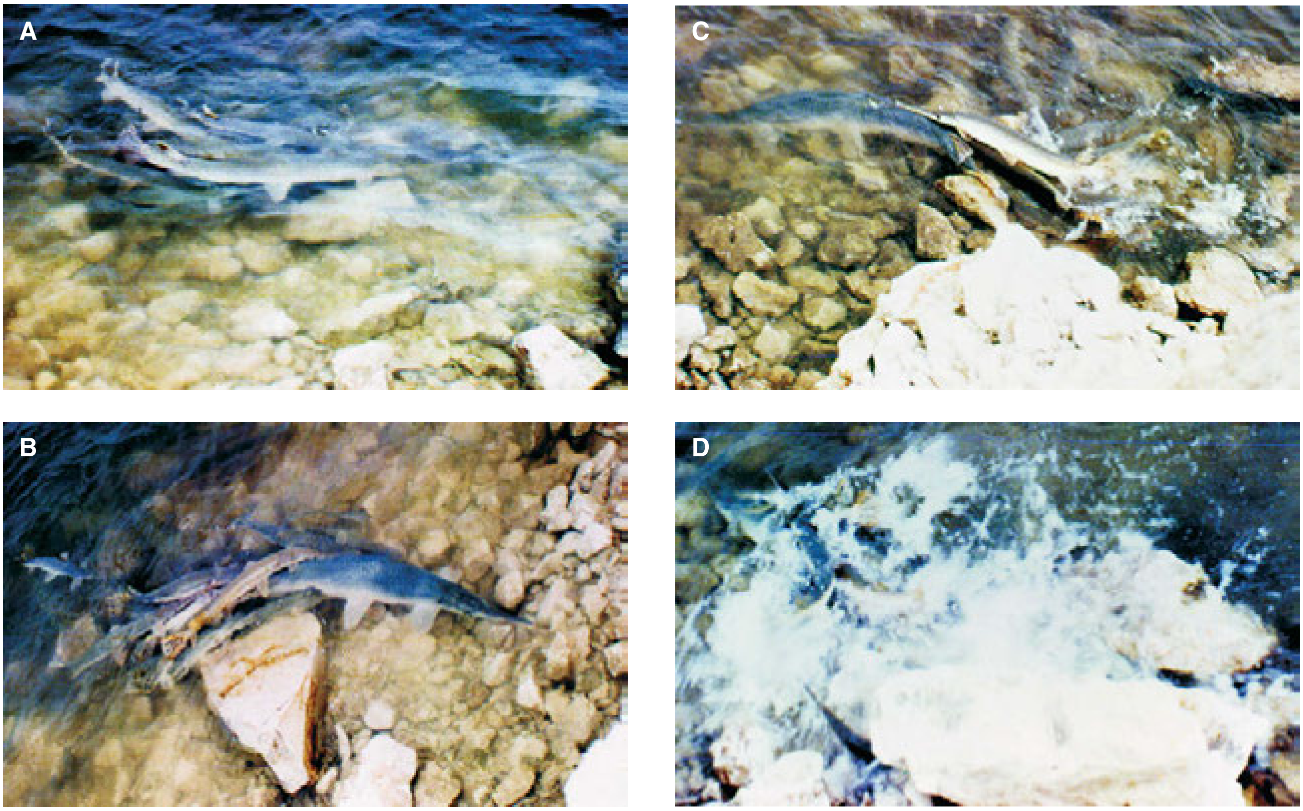

Figure 7.12. Courtship and spawning sequence in Longnose Gar, *Lepisosteus osseus*, May 1974, Lake Texoma, Oklahoma. *From top to bottom*: (A&B) Female (largest) and a group of smaller males entering the shallows; (C) members of the group starting to undulate while swimming in place; (D) violent thrashing of water, presumably accompanied by release of eggs and milt. A few eggs from this spawning event were thrown out of the water onto the shore (photographs by and used with permission of C. Taber).

lateral, nearly in-place, undulations with the males crowding closer and undulating alongside her. The undulations began relatively slowly, quickly increased in tempo with splashing of water, and suddenly ceased, after which the female's caudal fin was briefly visible slowly moving above the water surface before the group swam away. One group of 3 Spotted Gars spawned 5 times over a 30-min period in an area of about 8 m^2. Other reports of spawning in Spotted Gars mention it occurring in shallow, vegetated habitat during daylight hours (Tyler & Granger 1984; Love 2004).

Fecundity

Fecundity increases exponentially with increasing body length in Gars, resulting in large egg-count differences within and among species. Maximum count of mature eggs for Alligator Gars in the southeastern United States (557,390) was 7 times that (80,137) in Longnose Gars and 100 times that (5,587) in Spotted Gars (Ferrara 2001). The maximum counts for Longnose and Florida Gars in Ocala National Forest, Florida, were 77,156 from a 1,422 mm TL female and 15,450 from an 864 mm TL female, respectively (Holloway 1954).

Average counts of mature eggs include the following for different Gar populations: Florida Gars, 3,899 to 4,071 (Holloway 1954); Spotted Gars, 2,498 to 13,040 (Redmond 1964; Ferrara 2001; Love 2004; Smith 2008); Longnose Gars, 18,034 to 33,341 (Netsch & Witt 1962; Johnson & Noltie 1997; Ferrara 2001; McGrath 2010); and Alligator Gars, 157,291 (Ferrara 2001). The average number for different size-groups of Tropical Gars ranged from 23,907 for the smallest size range (651–700 mm TL) to 94,299 for the largest (1,151–1,200 mm TL; Mora et al. 1997).

Gametes

Sperm (spermatozoa) in Gars, as in other neopterygians (the Bowfin and teleosts), have no acrosome at the tip

(Jaroszewska & Dabrowski 2009). Unlike other neopterygians the sperm head is bullet-shaped rather than rounded. Otherwise no notable differences in sperm morphology exist between Gars and teleosts.

The eggs are demersal, adhesive, and often found attached singly to submergent vegetation or the bottom substrate. The eggs are large and often described as greenish or gray. In fertilized eggs, there is a white area that, in Longnose Gars, is about 2 mm wide and represents an area of yolk-free cytoplasm, the blastodisc, at the animal pole of the cell (Long & Ballard 2001). Measured egg diameter varies considerably among studies, even for the same species. For example, in Spotted Gars, the average was 3.0 mm in Louisiana (Love 2004) and 4.5 mm in Missouri (Redmond 1964). The averages for Alligator Gars are 2.1 mm (Ferrara 2001) in the southeastern United States and 4.1 mm in Mexico (Aguilera et al. 2002). Such large differences might be artifacts of methodology. In a comparative study of Spotted Gars, Longnose Gars, and Alligator Gars, average egg diameters were 2.3, 2.5, and 2.1 mm, respectively (Ferrara 2001). Immediately after fertilization, Longnose Gar eggs are spherical and have a measured diameter of 2.8–3.1 mm (Long & Ballard 2001). Sizes of fertilized eggs in Alligator Gars and Tropical Gars averaged 4.1 and 3.8 mm, respectively (Aguilera et al. 2002).

Once in water, the egg envelope swells, revealing a sticky, jelly-like outer layer that overlays the chorion, the outer egg membrane (Long & Ballard 2001). The chorion is underlain by a jelly-like perivitelline layer and then the plasma membrane of the egg. As in most actinopterygians, the egg has a single micropyle (a pore at the animal pole) that provides passage through the egg envelope for a single sperm to contact the egg's plasma membrane. After fertilization, a dimple in the plasma membrane at the apex of the blastodisc signifies the point of sperm entry.

Development

Developmental rate varies, of course, with temperature. For example, time from fertilization to hatching in Alligator Gars is only 48 h at 31°C (Aguilera et al. 2002), but Longnose Gars require 6–8 days at temperatures of 17–21°C (Long & Ballard 2001; Jaroszewska & Dabrowski 2009). The embryology of Longnose Gar was described in considerable detail by 19th-century biologists (Agassiz 1879; Balfour & Parker 1882; Dean 1895). The following account is based on Long & Ballard's (2001) descriptions for Longnose Gars with added details from a synthesis (Jaroszewska & Dabrowski 2009) of that study and both earlier and later work. In Long & Ballard's (2001) study, water temperatures were those of an outside water source in which the average of the morning and evening temperatures changed steadily from 17.0°C at fertilization to 21.5°C by hatching time 6 days later. Stages 1–29 were recognized between fertilization and hatching and stages 30–34 between hatching and absorption of the yolk sac.

Cleavage is meroblastic, as in teleosts, but not the Bowfin or other basal actinopterygians (this volume). During cleavage, furrows divide up the blastodisc (now called blastoderm). The furrowing in Gars, but not teleosts, is associated with grooves in the surface of the underlying yolk cell. By stage 5 (16–32 cells; 11 h), many of the grooves extend past the edges of the blastodisc and some reach around the yolk cell to the vegetal pole, but none cleaves the large yolk cell.

Blastula formation begins in stage 6 (64–512 cells) with tangential cleavages that produce complete blastomeres. In addition to division of the blasoderm itself, cell proliferation in the blastoderm includes budding of cells off of the underlying yolk cell. A result is an underlying yolk syncytial layer of cells incompletely separated from the yolk cell. This character otherwise occurs only in teleosts and elasmobranchs (Jaroszewska & Dabrowski 2009).

By the end of stage 8 (36 h) the blastula is complete, superficial blastomeres are tiny, and the blastoderm is a thin layer similar to that in teleosts. Gastrulation (epiboly) begins in stage 9 with cells proliferating as the blastoderm advances around the yolk cell. In epiboly, cells turn inward at the blastoderm edge and move as an underlying layer (hypoblast) between the upper blastoderm (epiblast) and the yolk cell. Epiboly begins with an indentation at a raised spot (dorsal lip) on the edge of the blastopore. The dorsal lip identifies the dorsal side of the embryo.

By stage 12, epiboly involves the entire edge of the blastoderm, which surrounds a large yolk plug (exposed surface of the yolk cell). By stage 15 (60 h), the yolk plug disappears, and there is an embryonic shield with a blastopore. Layers representing future endoderm and mesoderm develop from the hypoblast and the epiblast differentiates into future ectoderm and an enveloping, extra-embryonic layer of cells that serves a protective function and gives rise to no organs (Jaroszewska & Dabrowski 2009). The neural fold has developed and is starting to close from the posterior to the anterior end of the embryo. By the end of stage 19 (4 days), the tail bud forms, the first somites appear, and there is an external swelling anterior to the brain that forms during development of the adhesive organ (see morphology section).

At stage 20, the eyes have lenses, and the first mobility appears (slight lateral squirm). In stage 21, the heart is essentially straight, but begins to beat, the adhesive organ is conspicuous but not sticky, olfactory placodes are visible, and the first pigment appears (on the yolk sac and posteriodorsal to the eye). In stage 22, the dorsal fin fold is obvious and the intestine is visible between the yolk mass and the cloaca. In face-on view the adhesive organ is horseshoe shaped (convex edge up). The heart begins to coil and blood flows on the yolk sac. Motility increases to one or two coils.

In stage 23 (4.5 days) the somites are dusted with pigment. In stage 24, the adhesive organ is sticky, and the yolk mass is ovoid. In stages 25–27, pectoral fin buds become visible, and larvae swim in circles when removed from the chorion and prodded. By stage 28, rudiments (analgens) of anal and caudal fins appear in the ventral fin fold, the dorsal fin fold is eroded backward past the pectoral fins, and rudimentary gill filaments appear on the gill arches. The larva usually hatches at stage 29 (6 days). The analgen of the dorsal fin is clearly visible. The pectoral fins are half moon-shaped and by stage 30 they have transparent flanges. By the time the yolk sac is absorbed (stage 34), the pelvic fins have appeared, the median fins have rudimentary fin rays, the jaws are studded with sharp teeth, and the nasal sac has both incurrent and excurrent openings. Drawings of sequential stages from early prolarvae to pre-juvenile Longnose Gars are available (Heufelder 1982).

Early Life Stages

Gar early life history involves three distinct stages. The prolarva, or yolk-sac larva, has an externally visible yolk sac (Fig. 7.13; terminology from Hubbs 1943). The postlarva has no externally visible yolk sac, but the body form remains unlike the juvenile fish. We use the term “pre-juvenile” for the next stage, in which Gars have the general appearance of an adult but the opisthural (upper) lobe of the caudal fin forms a distinct, lance-shaped caudal filament (see see sixth paragraph below) that, except at its base, is free of the hypural (lower) lobe, the eventual caudal fin. The various stages grade into one another, and the size range during each stage may vary somewhat with species and rearing conditions but are roughly as follows (as TL): prolarvae, 7–20 mm; post-larvae, 16–35 mm; and pre-juveniles 30–270 mm (Wilder 1876; Suttkus 1963; Echelle 1967; Simon & Wallus 1989; Aguilera et al. 2002; Comabella et al. 2010).

Prolarval Gars initially have a short, blunt snout, dark optic cups visible through the head surface, small pectoral-fin buds, and scattered melanophores, particularly on the yolk sac (Simon & Wallus 1989; Aguilera et al. 2002; Comabella et al. 2010). A continuous median fin fold extends from somewhat posterior to the head around the tail to the yolk sac. The most distinguishing character is a disk-shaped adhesive organ on the snout that serves for attachment to objects in the water (Fig. 7.13; see behavior section).

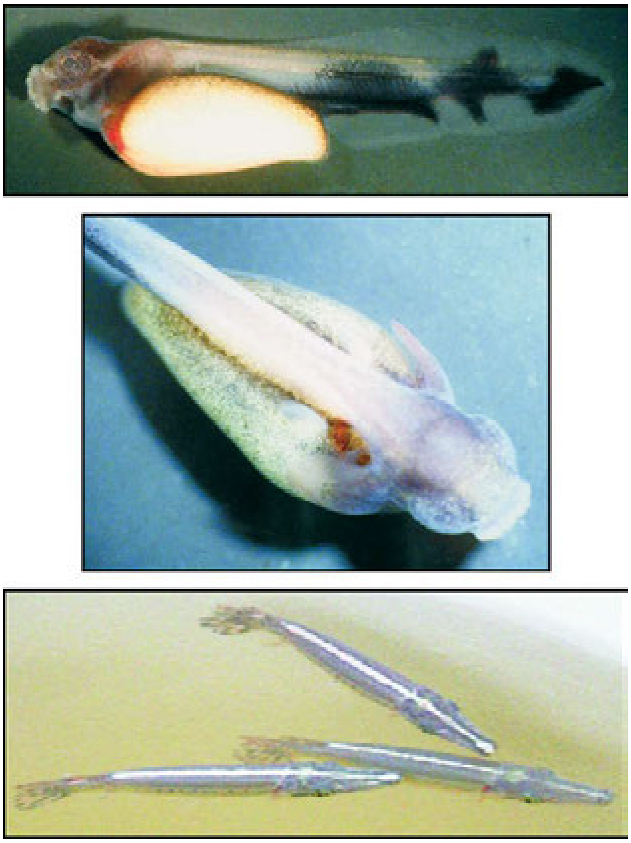

Figure 7.13. Young Alligator Gar, *Atractosteus spatula*. *Top*: Lateral view of a pro-larva at about stage 32 (about 12 mm TL; see development section). *Middle*: Dorsal view showing adhesive disc with papillae on snout; the large opercular flaps are visible just behind the head. *Bottom*: Prejuveniles (about 100 mm TL) (photographs by and used with permission of A. Ferrara).

The Gar adhesive organ is superficially similar to the adhesive organ of prolarval Bowfins; however, they seem to have fundamentally different embryological origins. In Gars the organ apparently originates as a single bulge in the cell layer (epiblast) that eventually becomes ectoderm (Beard 1889), but in Bowfins it is endodermal and begins as two diverticula of the embryonic foregut (Eycleshymer & Wilson 1908). In Gars, the organ has a number of pronounced papillae (Fig. 7.13) on the exposed surface (Agassiz 1879; Jollie 1984) that are absent in Bowfins.

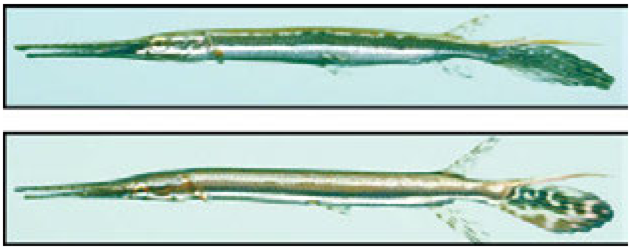

Figure 7.14. Top: Prejuvenile Longnose Gar, *Lepisosteus osseus* (89 mm SL). *Bottom*: Spotted Gar, *Lepisosteus oculatus* (109 mm SL), showing the caudal filament above the caudal fin that characterizes this stage of development (photograph by and used with permission of Stephen T. Ross from Ross 2001).

At hatching in Longnose Gars, the adhesive disc has about 30 papillae (Balfour & Parker 1882), which Agassiz (1879) erroneously considered individual suckers. The organ has been variously referred to as a sucking disc (Agassiz 1879), an adhesive sucker (Suttkus 1963), or a suctorial disc (Mansueti & Hardy 1967). Histological studies, however, indicated long ago that the papillae are secretory not suctorial (Balfour & Parker 1882). In recent years, the adhesive organ and similarly functioning structures in other vertebrates have been called cement glands (Pottin et al. 2010). The adhesive organ effectively disappears in Gars by the time the yolk sac is absorbed (Mansueti & Hardy 1967; Long & Ballard 2001).

In post-larval Gars, the adhesive organ disappears early on, the snout elongates, and pelvic fins are visible. The caudal fin is heterocercal with the upper and lower portions of the larval caudal fin differentiated into dorsal and ventral lobes. The notochord extends straight back, or with a slight upward turn, as the axis of the dorsal lobe and reaches well past the lower lobe, which by now possesses fin rays.

The color pattern is particularly striking in post-larval Alligator Gars. The head and body are largely black except for a “vivid,” white, arrow-shaped area medially on top of the head, and white dorso-lateral markings on the body (Moore et al. 1973:343) that vary somewhat in degree of expression (Aguilera et al. 2002). Post-larvae of the congeneric Tropical Gars have similar, but less conspicuously white, markings on the head and body (Aguilera et al. 2002), and no white dorsal pattern occurs in Cuban Gars (Comabella et al. 2010). The white markings identify Alligator Gars at this stage. Longnose Gars, Spotted Gars, and Shortnose Gars differ from each other in the distribution of subdermal dorso-lateral pigmentation, density of external melanophores in various regions of the body, and modal differences in myomere counts (Wallus & Simon 1989, based mostly on post-larvae in Ohio River).

Pre-juvenile Gars of both genera have the overall body form of adults except for a unique locomotory structure, the caudal (or notochordal) filament (Fig. 7.14). When Longnose Gars are about 35 mm TL, the caudal fin is abbreviate-heterocercal, but the upturned notochord extends beyond the dorsal caudal fin base, forming the core of the functionally and structurally independent caudal filament (see behavior section). The filament has laterally flattened and transparent upper and lower vanes and striated muscle on the two sides of the notochord (Carpenter 1995). The filament is retained in the non-atrophied state until the fish is about 230–301 mm TL with variation among individuals and species (Riggs & Moore 1960; Suttkus 1963; Echelle 1967). Atrophied, non-functional remnants were recorded for individuals at 271, 281, and 305 mm TL in Shortnose Gars, Spotted Gars, and Longnose Gars, respectively (Wilder 1877; Echelle 1967). Average sizes at loss of the filament in laboratory-reared Spotted Gars and Longnose Gars (Riggs & Moore 1960) were 236 (range 210–250) and 279 mm TL (range 247–301), respectively.

Pre-juvenile Alligator Gars (35–50 mm TL) have a “brilliant,” mid-dorsal white stripe extending from tip of snout to origin of dorsal fin (Fig. 7.13; Aguilera et al. 2002:902). A similar stripe was described for individuals at 103 and 117 mm TL (May & Echelle 1968); it apparently disappears sometime between those sizes and 130 mm TL (Aguilera et al. 2002). The stripe is absent in the congeneric Tropical Gars (Aguilera et al. 2002) and Cuban Gars (T. García pers. comm.). Pre-juvenile Longnose Gars, Spotted Gars, Shortnose Gars, and Florida Gars have a dark lateral band (Fig. 7.14) that is more uneven (scalloped) on the dorsal edge in Longnose Gars than in the other species (Suttkus 1963).

By the time Alligator Gars are 35–50 mm TL and Tropical Gars are 60 mm TL, they have adult proportions of 15% and 18%, respectively, of snout length relative to TL (Aquilera et al. 2002). This separates them from the species of *Lepisosteus* that have much narrower and longer snouts. By 50 mm TL, the Longnose Gar is separated from all other *Lepisosteus* by its extremely narrow snout; jaw length is 13.0–25.5 times the minimum jaw width behind the nares versus 4.5–11.0 in the 3 other species (Suttkus 1963).

ECOLOGY

Habitat

Gars primarily inhabit quiet waters with sluggish or no flow in a diversity of situations ranging from lakes and streams to swamps, bayous, tidal creeks, and shallow estuarine bays and sounds (Fig. 7.11). Spotted Gars and Florida Gars often are common in shallow, more heavily vegetated waters, but adult Longnose Gars and Alligator Gars seem to be more common in deeper, less vegetated habitats (Goodyear 1966; Robertson et al. 2008). The Shortnose Gar is sometimes abundant in seasonally flooded oxbows and slow backwaters (M. L. Warren, pers. comm.), but it might prefer open-river situations. According to Cross (1967) it occurs primarily in larger riverine habitat and appears to avoid the quiet-water situations occupied by Spotted Gars and Longnose Gars. Becker (1983:241) said it prefers "open, slow-moving, silty rivers."

Longnose Gars and Spotted Gars showed marked habitat partitioning in a coastal-plain section of the Brazos River, Texas (Robertson et al. 2008). Most (84%) of the Longnose Gars were taken from the river channel and 98% of the Spotted Gars were from oxbow lakes. The oxbow abundances of Longnose Gars increased during flood connections with the river, apparently in response to food availability. Adult Alligator Gars (n = 2; 1,474–1,850 mm TL) only occurred in the river and juveniles (n = 16; 409–810 mm TL) only in oxbows. Similar habitat partitioning among species was indicated in a survey of coastal waters in Mississippi (Goodyear 1966), where Longnose Gars and Alligator Gars were mostly in the larger rivers and bayous and estuarine bays and sounds and Spotted Gars were primarily in smaller bayous and lakes.

Diet: Larvae and Juveniles

From the earliest stages after yolk sac absorption, natural feeding activity in young Gars is based primarily on living prey. In laboratory tanks, however, larval Alligator Gars can be reared on artificial foods alone, especially if the food floats or is small enough to remain suspended in the water column (Mendoza et al. 2008a; Clay et al. 2011).

The earliest foods usually are primarily entomostracans (cladocerans and copepods) and aquatic insect larvae (Forbes & Richardson 1920; Cahn 1927; Echelle 1968; Echelle & Riggs 1972), but fishes become important early in development. The stomachs of 10 post-larval Longnose Gars in the earliest feeding stage (17–21 mm TL) from Lake Texoma, Oklahoma, had 62 cladocerans, 18 copepods, 5 midge larvae (Diptera), 1 midge adult, and 3 fish larvae (Echelle 1968). In 12 Longnose Gars of the same size range from the Ohio River, Kentucky, fish larvae occurred in 7 stomachs and were the only food items detected; in the following year, cladocerans occurred in all 17 of the smallest Longnose Gars examined (22–24 mm TL), but there were no fishes (Pearson et al. 1979).

Piscivory at an early age seems especially pronounced in the Longnose Gar. About 70% of 56 Longnose Gars 17–36 mm TL from Lake Texoma had fishes in their stomachs (Echelle & Riggs 1972). Similarly, in the Ohio River, fishes occurred in 84% of 132 Longnose Gars 17–36 mm TL (Pearson et al. 1979). In contrast, fishes occurred in only 8% of a similar-sized (15–34 mm) combined group of 34 Spotted Gars and Shortnose Gars from Lake Texoma (Echelle & Riggs 1972).

In 768 post-larval to large pre-juvenile Gars in Lake Texoma, fishes appeared in 75% and 95% of stomachs with food in individuals of 15–114 mm TL and 115–306 mm TL, respectively (Echelle 1968; Echelle & Riggs 1972). The remaining items in both size-groups were primarily entomostracans and midge larvae. Fishes represented 100% of the animal items eaten by 17 young Longnose Gars (119–269 mm TL) in Missouri (Netsch 1964). Also in Missouri, fishes occurred in 82% of Spotted Gars 50–74 mm TL and in 100% of those 100–124 mm TL (Redmond 1964).

A high degree of surface feeding is indicated by the observation that small Gars often consume inordinate numbers of a cladoceran (*Scapholebris* spp.) specialized for living and feeding on the underside of the surface film. Gars <50 mm TL in Lake Texoma (Echelle 1968; Echelle & Riggs 1972) and small Longnose Gars in Illinois (Forbes & Richardson 1920) were often filled with this cladoceran. In Lake Texoma, it represented 90% of the 1,189 cladocerans in small Gars (15–116 mm TL). *Scapholebris* also was the most abundant cladoceran in Longnose Gars <61 mm TL from Lake Mendota, Wisconsin, and was second only to fishes in importance (Haase 1969).

The earliest fish foods in young Gars in Lake Texoma were primarily larval Mississippi Silversides (*Menidia audens*) and young-of-the-year of this species dominated the diet throughout the first few months of life (Echelle & Riggs 1972). This small fish, which represented 82% of the 175 fish items identified, is the most abundant fish in shallow waters of Lake Texoma (Hubbs 1984). It forms dense schools and tends to rest at the surface at night, when young Gars are feeding more actively (Echelle 1968). Similar behavior in the Brook Silversides (*Labidesthes sicculus*) makes it particularly susceptible to predation by Longnose Gars (Hubbs 1921). Other fishes identified from young Gars in Lake Texoma were, in decreasing order of abundance, Western Mosquitofishes (*Gambusia affinis*), shad (*Dorosoma* spp.), Common Carp (*Cyprinus carpio*), micropterine bass (*Micropterus* sp.), Freshwater Drum (*Aplodinotus grunniens*), shiners (*Notropis* spp.), Sunfishes (*Lepomis* spp.), and a Gar (*Lepisosteus* sp.). Pan fishes and gamefishes (*Micropterus* spp. and *Lepomis* spp.) occurred in only 2.3% of the stomachs.

Diet: Adults

Except for brief reports on foods of Tropical Gars (Reséndez & Salvadores 1983; Mora et al. 1997), knowledge of the diets of Gars is based on the five North American species. Some general trends are that all species are predators, primarily on fishes and macroinvertebrates, fishes generally are the predominant food items, the smaller species consume smaller items, the Longnose Gar is more piscivorous than the others, and the Alligator Gar seems to scavenge for food more than the others (Darnell 1961; Goodyear 1967; Seidensticker 1987; Robertson et al. 2008). Of course, availability is important in determining diet. For example, Spotted Gars consumed only crayfishes during a drying period in an oxbow on the Brazos River, but in another oxbow they at times were consuming only shad (Robertson et al. 2008). Thus, dietary differences between species might be more a function of opportunity than any innate dietary preference (Robertson et al. 2008).

Prey behavior and habitat structure have interacting effects on predation efficiency in Spotted Gars (Ostrand et al. 2004). In experiments with simulated vegetation density, Spotted Gars preyed more efficiently on Fathead Minnows (*Pimephales promelas*) than on Bluegills, regardless of stem density. Predation on Fathead Minnows and Bluegills was unaffected and negatively associated, respectively, with stem density.

The largest early survey of adult Gar foods revealed a remarkable diversity of fish items (Lagler & Hubbs 1940). In this study of Longnose Gars in streams and lakes in southern Michigan, 136 Gars with food in the stomach had eaten 23 identifiable fish species. Non-fish taxa (crayfishes and insects) formed only 7% of the items. Game and pan fishes, including Yellow Perch (*Perca flavescens*), Sunfishes, and bullheads (*Ameiurus* spp.), represented 18% of the identifiable fishes. The remaining 92% consisted primarily of cyprinids (58%), Brook Silversides (6%), Brindled Madtoms (*Noturus miurus*; 6%), and Logperch (*Percina caprodes*; 8%).

Longnose Gars generally feed primarily on non-game forage fishes. For example, Menhadens (*Brevoortia patronus*) were dominant (83%) in a brackish-water population in Mississippi (Goodyear 1967), shad were 60 and 81% of the items in lakes in central Florida (Crumpton 1971) and a Texas reservoir (Seidensticker 1987), respectively, and shad and Red Shiners (*Cyprinella lutrensis*) were dominant (about 90%) in an Oklahoma reservoir (Tyler et al. 1994). Shad were most important in Longnose Gars from the Brazos River, Texas, except in a dry year when shad declined in the diet and mayflies and North American Catfishes were more important (Robertson et al. 2008). Unusual items in Longnose Gar stomachs include bones and feathers, probably from a duck, and a fishing bobber (Crumpton 1971).

The smaller species of *Lepisosteus* seem to ingest more invertebrates than do Longnose Gars, although fishes are consistently important items. In Florida's Tamiami Canal, invertebrates occurred in 58% of the Florida Gar stomachs containing food (Hunt 1954). These were mostly freshwater shrimp (*Palaeomonetes*), but crayfishes and insects were included. Fishes, primarily oviparous cyprinodonts (killifish) and Livebearers (Poeciliidae), occurred in 70% of the stomachs. A diet dominated by fishes (primarily shad and Western Mosquitofishes), freshwater shrimp, and crayfishes also occurred in Spotted Gars from Missouri (Redmond 1964). Spotted Gars in bayous near the Mississippi coast consumed primarily small crabs (*Uca pugnax* and *Callinectes sapidus*), followed by prawns (*Penaeus* sp.), freshwater shrimp, and Menhadens (Goodyear 1967). Crayfishes (*Procambarus*) were the most frequent item in collections of Spotted Gars in Texas rivers (Bonham 1940) and a floodplain lake in Louisiana (Snedden et al. 1999). In both studies, crayfishes were followed by Sunfishes and shad as the most abundant food. Crayfishes were the most important items in one oxbow on the Brazos River and shad were dominant in another (Robertson et al. 2008). In an Oklahoma lake, fishes, crayfishes, and insects composed 68, 16, and 16%, respectively, of the food items (Tyler & Granger 1984). In Shortnose Gars from an Iowa lake, fishes and crayfishes represented 60 and 40%, respectively, of the items (Potter 1923).

Like all Gars, Alligator Gars are primarily piscivorous, but they seem more likely to scavenge for food, to feed on bottom-dwelling species (Fig. 7.10), and to feed on birds. Foreign items in the stomachs have included a variety of fishing hooks and lures, a steel fish-stringer, a trash bag, a chicken probably taken from a baited crab line, and even a thermostat from a diesel engine (Goodyear 1967; Seidensticker 1987). In a coastal fishing locality, they fed heavily on aggregations of Hardhead Catfishes (*Ariopsis felis*) feeding on shrimp-boat refuse (Goodyear 1967). In Sam Rayburn Reservoir, Texas, they fed primarily on bottom-feeding fishes >20 cm TL, including Gizzard Shad (*Dorosoma cepedianum*), Freshwater Drums (*Aplodinotus grunniens*), Channel Catfish (*Ictalurus punctatus*), and Suckers (Catostomidae). In the same study, Longnose Gars were selective for smaller prey that were higher in the water column, primarily Threadfin Shad (*Dorosoma petenense*), but both Longnose Gars and Alligator Gars fed on a wide variety of fishes (Seidensticker 1987). Observations of birds in the diet of Alligator Gars include the capture and swallowing of a perched Anhinga (*Anhinga anhinga*) and the presence of American Coots (*Fulica americana*) in the stomachs (Raney 1942; Seidensticker 1987).

Little is known about food habits in the other members of the genus *Atractosteus*. Stomachs of Tropical Gars from Mexico (Reséndez & Salvadores 1983) and Costa Rica (Mora et al. 1997) contained primarily cichlid and poeciliid fishes. The list of identified fishes from the Costa Rican population included a cichlid (*Cichlasoma = Parachromis managuense*, Jaguar Guaporte), a poeciliid (*Poecilia gillii*), a Catfish (*Rhamdia quelen* as *R. guatemalensis*, South American Catfish), two species of Characins (*Astyanax fasciatus*, Banded Astyanax, and *Roeboides guatemalensis*, Guatemalan Headstander), and a gymnotid (*Gymnotus cylindricus*). The Mexican population appears to show a juvenile-to-adult shift from piscivory toward greater omnivory with significant amounts of vegetable matter in the stomachs (Reséndez & Salvadores 1983).

Diel Feeding Periodicity

Gars generally are thought to feed more actively at night than during the day. Based on four stages of the condition of stomach contents, adult Longnose Gars in Mississippi coastal areas fed primarily from 1800 to 0600 h, and little feeding occurred from 0600 to 1800 h (Goodyear 1967). Spotted Gars showed no such difference. Instead, they fed more heavily during incoming or high tides than during receding or low tides (Goodyear 1967). In contrast, radio-tracked Spotted Gars in Louisiana showed greater activity at night, and in an October collection, stomachs collected at night had three times as many food items as those collected during the day (Snedden et al. 1999). Young Longnose Gars collected at night had a lower frequency (25%) of empty stomachs than those collected in daylight (41%; Echelle 1968), and adult Tropical Gars feed mainly at night (Reséndez & Salvadores 1983). Finally, in the laboratory, Florida Gars were inactive in relatively bright light but began pursuing food fish when illumination was reduced to dusk-like levels (Hunt 1960).

Demography: General Notes

Like many animal groups, demographic variation among Gar species is associated with differences in body size. The large species mature later and have lower mortality rates and greater longevity. In a study of Spotted Gars, Longnose Gars, and Alligator Gars in the southeastern United States, the smallest species, Spotted Gars, matured earlier, grew faster, died at younger ages, and had lower fecundity and lifetime reproductive output compared with the other two (Ferrara 2001). The Longnose Gar was intermediate for these traits. The body size–related differences between species are paralleled by differences between the sexes in which females are larger, mature later, and live longer than the males (see reproduction section and demography age and growth subsection of ecology section).

Demography is expected to vary with degree of human exploitation, and this seems to apply to Alligator Gars in the southeastern United States (Ferrara 2001). The most heavily exploited of three study populations (Lake Pontchartrain) showed lower survivorship, lower lifetime reproductive output, lower population growth rates, and truncated age and size distributions compared with two other populations.

Demographic studies of Gars usually are based on annuli (growth rings) in the saggitta (largest otolith of the inner ear), or more often, one of the two outermost branchiostegal rays (slender, thin bones supporting the gill membranes). Ferrara (2001) preferred otoliths because branchiostegal-ray annuli were difficult to detect in larger Alligator Gars and Longnose Gars, but Murie et al. (2009) considered branchiostegal rays more reliable in the Florida Gar. Distinguishing annuli from false annuli produced during periods of stress or low food availability can confound interpretation, resulting in under- or overestimation of age. Finally, no rigorous validation (Campana 2001) of age estimates is available for any population of Gars. Despite these problems, age and growth studies provide valuable insight into demography of Gars.

Demography: Growth Rates in Larvae and Juveniles

The initial growth rates are faster in larger species of both Gar genera. This is demonstrated for *Atractosteus* in a study of laboratory-reared Alligator Gars and the smaller Tropical Gar (Aguilera et al. 2002). Size at hatching was similar in the two species (range 6.6–9.0 mm TL). By the time the yolk sac was absorbed, 5 days after hatching (DAH) in Alligator Gars and 5–6 DAH in Tropical Gars, the size ranges did not overlap with Alligator Gars at 14.2–19.2 mm TL and Tropical Gars at 12.5–13.8 mm TL. By 15 DAH, Alligator Gars were at 34.8–50.0 mm TL, but Tropical Gars did not approach that size range until 7 days later (22 DAH), when they were at 22.0–36.0 mm TL.

A similar pattern is seen in laboratory-reared *Lepisosteus* with late pre-juvenile and early juvenile Longnose Gars showing about twice the rate of growth seen in similar-sized Spotted Gars (Riggs & Moore 1960). In these fish, which initially ranged from 189 to 369 mm TL, the growth rate over a 25-day period was 3.2 mm/day (range 2.3–4.5 mm/day; n = 5) for Longnose Gars and 1.7 mm/day (range 1.4–2.1 mm/day; n = 6) for Spotted Gars. Average weight gain was 1.8 and 1.0 g/day, respectively. A similar growth rate for Longnose Gars (3.0 mm/day) occurred in a 52-day study (Netsch & Witt 1962) in which 20 fish went from an average of 136 mm TL (range 99–159 mm TL) to 290 mm (range 263–325 mm TL). The only direct record of growth in non-laboratory conditions is from a single Longnose Gar maintained for 165 days in semi-natural conditions with no supplemental feeding (Matthews et al. in press). This Gar grew at an average rate of 1.6 mm/day and reached 261 mm TL between the time it originated from a natural spawning in Lake Texoma (18 May) and the time (31 October) it was captured from a small (200 cm long, 140 cm wide, and 25 cm deep) ornamental pool where it had been introduced shortly after hatching in the laboratory.

Demography: Age and Growth

Female Gars live longer and attain larger sizes than males. The sexes are about equal in body length at ages 1–2, but males approach their maximum size earlier than females, and this, together with greater female longevity, means that the females reach greater sizes (Netsch & Witt 1962; Ferrara 2001; Love 2004; DiBenedetto 2009; Murie et al. 2009; McGrath 2010). This is especially pronounced in the larger species. For example, in Louisiana, age-2 Alligator Gars of both sexes were at about 1,000 mm TL, but by age 10 the averages were 1,300 mm for males and 1,587 mm for females (DiBenedetto 2009). The largest male and female collected were 1,495 and 2,120 mm TL, respectively, and the female was 3 times heavier than the male (68 versus 20 kg). Maximum ages estimated from otoliths were 16 for males and 26 for females. The oldest Gar in age and growth studies seems to be a female Alligator Gar estimated at 50 years old; the oldest male in the same report was 26 years old (Ferrara 2001).

In Longnose Gars, females are larger than males after 1–3 years of age (Alabama, Ferrara 2001; Kansas, Klaasen & Morgan 1974; Missouri, Netsch & Witt 1962; Johnson & Noltie 1997; Virginia, McGrath 2010; Wisconsin, Haase 1969). In a large sample (n = 689) from Virginia, both sexes often reached 400 mm TL by age 1 (McGrath 2010). By age 10, however, the averages were about 800 mm TL for males and 1,000 mm TL for females, and females were >2 times as heavy (about 36 versus 16 kg). Maximum ages estimated for Longnose Gars are 29 years for males and 32 for females in Wisconsin (Haase 1969). Most estimates are somewhat lower; the next highest (males 22, females 27) is from the large Virginia sample (McGrath 2010).

Spotted Gars reached greater body sizes in an Oklahoma lake (Tyler and Granger 1984) than in two Louisiana locations, a Lake Ponchartrain estuary (Love 2004) and the upper Barataria Estuary (Smith 2008). Maximum lengths of males and females were 809 and 1,030 mm TL in the Oklahoma sample, and 585 and 729 mm TL across the 2 Louisiana samples, respectively. The maximum estimated age for sampled males and females was 5 and 6 years in Barataria Estuary and 8 and 10 years for the Lake Ponchartrain estuary, respectively. The maximum age estimated for Spotted Gars is 18 years for a female 910 mm TL in southeastern Missouri (Redmond 1964).

The life history traits of Florida Gars showed significant differences between two populations in the Florida Everglades, especially for males (Murie et al. 2009). At 2–3 years of age, both sexes were about 400 mm TL, but in older age-classes, females were larger than males, and the population differences were more pronounced. Maximum ages (estimated from branchiostegal rays) for the two populations were 5 and 10 for males and 17 and 19 years for females. Interestingly, the population with the larger, more rapidly growing females showed the reverse for males, which showed lower growth rate, survivorship, and maximum age than males of the other population. The largest male and female in this study were about 525 and 800 mm TL, respectively. Holloway (1954) reported maximum TL of 660 mm (males) and 864 mm (females) for Florida Gars.

Apparently only one study provides information on age and growth in Shortnose Gars. The largest individual in a sample of 118 from the Wabash River, Indiana-Illinois, was 776 mm TL and weighed 1.9 kg (Sutton et al. 2009). The oldest age-estimate from this sample was 12 years. These estimates of maximum size and age probably were from females, although the fish were not separated by sex.

Demography: Length-Weight Relationships

The precise relationship between body length and weight is affected by a variety of variables. For example, seasonal variation reflecting gonadal condition apparently occurred in Spotted Gars (Redmond 1964). A survey of 15 reservoir populations (sexes combined) of Spotted Gars found that 2% of the variation was attributable to differences among populations and 6% was not attributable to body length or reservoir effects (Pope & Wilde 2003).

Gars show little sexual difference in length-weight relationship and the sexes often are lumped in such analyses without testing for a difference. Slight differences, however, can occur. In three separate studies, male Spotted Gars were slightly heavier than females of the same length (Redmond 1964; Love 2004; Smith 2008), and the reverse occurred in a fourth study (Tyler & Granger 1984). In Tropical Gars, length-weight curves indicated that males >450 mm TL were slightly heavier than same-sized females, but the reverse was true at shorter lengths (Mora et al. 1997). No statistically significant difference between the sexes was detected in Florida Gars (Murie et al. 2009), Longnose Gars (McGrath 2010), or in two separate populations of Alligator Gars (Garcia de León et al. 2001; DiBenedetto 2009).

Demography: Survivorship

Because of smaller size and lower longevity, male Gars should have higher estimates of annual mortality than the females. This was the case for two populations of Florida Gars (Murie et al. 2009). Estimated annual survival for female Florida Gars at two localities was similar, and the rate for the lumped sample was 81% (Murie et al. 2009). The rates for males (58% and 73%) at the two localities were significantly different from each other and from the female rate. Other studies of survivorship have combined the sexes.

Large species of Gar should show higher annual survival rates than small species, and this seems to apply to Gars in the southeastern United States. The estimated annual survival rates (sexes combined) for two populations of Spotted Gars were 16.8% (Smith 2008) and 51% (Ferrara 2001). The estimate for a population of Longnose Gars was 70% (Ferrara 2001), and the estimates for four populations of Alligator Gars (sexes combined) ranged from 80% to as high as 97% (Ferrara 2001; DiBenedetto 2009).

Demography: Population Sizes and Densities

The only estimate of Gar population density seems to be a mark-recapture study of Spotted Gars in a 6.6 ha lake in the Atchafalaya River basin, Louisiana (Bonvillain et al. 2008). The estimated density was 315 Gars/ha (95% confidence interval [CI] 127–788). Biomass density was 267 kg/ha (CI 109–668). These are bank-full estimates and the densities during low water periods are likely much greater (Bonvillain et al. 2008).

Predation

Adult Gars have few predators other than humans. This is largely due to their size and a nearly impenetrable protective armor of thick ganoid scales and heavy skull bones. Anecdotal observations indicate that the American Alligator (*Alligator mississippiensis*) at least occasionally preys on Gars (Spitzer 2010), and an analysis of 411 stomachs yielded a 2.6% frequency of occurrence of Gar remains (Valentine et al. 1972). River Otters (*Lontra canadensis*) also feed on Gars (Smith 2008).

Small Gars undoubtedly are preyed on by many aquatic animals, including other Gars. For example, a 28 mm TL Spotted Gar occurred in a 60 mm TL Spotted Gar (Redmond 1964), a Gar occurred in the stomach of a small Longnose Gar (Echelle 1968), 3 Spotted Gars ranging from 510 to 610 mm TL were in Alligator Gar stomachs (Seidensticker 1987), and Gars (*Lepisosteus* spp.) represented 25% by volume of the stomach contents in a small sample (9 with food) of Alligator Gars (Robertson et al. 2008). Cannibalism in Alligator Gars starts by at least 20 DAH when individuals average <50 mm TL (Mendoza et al. 2002; Clay et al. 2011). In laboratory tanks starting with 5-day-old larvae, mortality due to cannibalism was 19–44% after 15 days (Clay et al. 2011).

Predation on eggs and prolarvae might be reduced by the Gar toxin present in these stages of development (see physiology section). Birds and crayfishes and other crustaceans are susceptible to the toxin, and chickens, at least, resist eating the eggs. Many potential aquatic predators (fishes, frogs, turtles) are not susceptible to the toxin, and fishes readily eat the eggs.

Parasites

A total of 41 parasite species are identified from lepisosteids (Table 7.3). These include 14 trematodes, 4 cestodes, 7 nematodes, 2 acanthocephalans, 2 isopods, 5 copepods

Table 7.3. Parasites of North American Gars. Hoffman (1999) is the authority except where indicated by superscripted numbers and except for the bivalve records, which were taken from OSUDM (2006). All bivalve records are based on instances of observed metamorphosis of glochida from Gar infestations. Superscripted numbers are: 1 = Salgado-Maldonado et al. 2004; 2 = Tkach et al. 2010; 3 = Tkach et al. 2008; 4 = Moravec & Salgado-Maldonado 2003; and 5 = Bowman et al. 1977.

	Species					
Parasite	**Alligator Gar**	**Tropical Gar**	**Longnose Gar**	**Spotted Gar**	**Florida Gar**	**Shortnose Gar**
Trematoda						
Apophallus venustus			X			
Bucephalopsis gracilescens			X		X	
Clinostomum complanatum		X[1]	X			
Diplostomum sp.		X[1]				
Macroderoides spiniferus			X	X	X	X
Macroderoides texanus	X[2]					
Odhneriotrema incommnoum					X	
Paramacroderoides echinus			X		X	X
Paramacroderoides kinsellai				X[3]	X[3]	
Paramacroderoides pseudoechinus					X	
Perezitrema bychowskyi		X[1]				
Plesiocreadium parvum			X			
Posthodiplostomum minimum		X[1]			X	
Rhipidocotyle lepisostei	X					
Cestoda						
Bothriocephalus sp.				X		
Proteocephalus ambloplitis	X		X	X		X
Proteocephalus perplexus			X		X	X
Proteocephalus singularis		X[1]	X		X	X
Nematoda						
Camallanus sp.					X	
Contracaecum sp.		X[1]				
Contracaecum spiculigerum	X		X	X	X	X
Cystidicola lepisostei			X			
Cystoopsis atractostei		X[4]				
Dichelyne lepisosteus	X					
Eustrongylides sp.			X		X	
Spiroxys sp.		X[1]				
Acanthocephala						
Leptorhynchoides thecatus			X		X	X
Neoechinorhynchus cylindratus			X			
Hirudinea						
Placobdella montifera			X			
Crustacea						
Anilocra acuta (isopod)	X[5]		X			
Argulus lepidostei			X		X	X
Argulus mississippiensis			X			X
Argulus sp.				X		
Ergasilus elegans			X		X	X
Ergasilus versicolor (or *arthrosis*)	X		X			X
Nerocilia lanceolata (isopod)	X		X			
Lernaea sp.					X	
Lernaea variabilis						X
Mollusca (Bivalvia)						
Amblema plicata						X
Crytonaias tampicoensis			X			
Elliptio buckleyi					X	
Lampsilis floridensis			X		X	
Lampsilis radiata					X	
Lampsilis teres	X		X			X

(anchor worms), and 1 leech. Possibly reflecting intensity of study, 24 (59%) of the reported parasites are from Longnose Gars, followed by Florida Gars with 18 and Shortnose Gars with 14. The remaining 3 Gar species had 5–9 reported parasites. Thirteen parasite species are reported from ≥2 species of Gars. The parasites representing potential specialists on Gars include three trematodes, *Macroderoides spiniferus*, *Paramacroderoides echinus*, and *Perezitrema bychowskyi*, and two nematodes, *Dichelyne lepisosteus* and *Cystoopsis atractostei* (Salgado et al. 2004). The average species richness of parasites in individual Gars seems low relative to most other fishes at least in part as a result of their top-predator status (Salgado et al. 2004). Top predators encounter fewer intermediate hosts than do more generalist feeders, possibly helping to explain the relatively low numbers of parasite species on individual Gars.

CONSERVATION

Gars have often been treated as destructive elements of aquatic systems in the United States (Scarnecchia 1992), and fisheries management programs based on this premise have focused on reducing Gar populations (Burr 1931; Seidensticker & Ott 1989; Magnuson & Lathrop 1992). Only in the last few decades have efforts been directed at protecting Gar populations.

Although the Spotted Gar is listed as federally Endangered in Canada, no Gar species is included on the IUCN Red List and most species are reasonably abundant in at least some parts of their range. Some species, however, are regarded as Extirpated or Critically Imperiled at the margins of their ranges. For example, the Alligator Gar is listed as Extirpated from Ohio and Indiana, Likely Extirpated from Illinois, and Imperiled or Critically Imperiled in seven states; the Spotted Gar is Extirpated from New Mexico and considered Imperiled or Critically Imperiled in three states; and the Shortnose Gar is listed as Extirpated from Pennsylvania and Alabama and Critically Imperiled in Montana, Ohio, and South Carolina (NatureServe 2010). Tropical Gar populations have declined, at least in local areas, in Mexico (Aguilera et al. 2002; Mendoza et al. 2002) and Costa Rica (Mora 1997; Aguilera et al. 2002).

A consortium of research and management scientists, the International Network for Lepisosteid Fish Research, was established to facilitate communication among academics and game and fish management professionals from Canada, Cuba, Mexico, Meso-America, and the United States. The program for a 2010 joint meeting of this group and the Alligator Gar Technical Committee of the Southern Division of the American Fisheries Society indicates a high degree of planning and research activity in the management, culture, and basic biology of Gars. A major management focus is on captive rearing and release of Alligator Gars and Tropical Gars, both of which are declining in areas of Mexico and Central America, respectively, where they are significant sources of food (see economic importance section). Programs aimed at culturing and improving techniques for the rearing of *Atractosteus* are underway in the United States, Mexico, Cuba, and Costa Rica (Mendoza et al. 2008b). Efforts in the United States also include stricter state limitations on harvest and in some states restoration and enhancement of populations of Alligator Gars.

The Alligator Gar seems to be the Gar most at risk for the relatively near future. Populations have declined throughout the species' range and in some areas a shift of the size range toward smaller sizes is indicated (Ferrara 2001; Mendoza et al. 2002). The species is considered vulnerable to extirpation from much of its historical range (Warren et al. 2000; Jelks et al. 2008). Suggested causes include loss of habitat for prey species (e.g., crabs in Lake Pontchartrain) and loss of floodplain spawning habitat and nurseries (O'Connell et al. 2007). Specific causes are difficult to identify, but dams, channelization, and levee construction on rivers and tributary streams clearly have eliminated many wetlands and reduced connectivity between the larger, more open habitats of the adults and the wetlands necessary for reproduction (Robison & Buchanan 1988; Etnier & Starnes 1993). A decline of about 99% occurred in trawl and beach-seine captures in Lake Pontchartrain, Louisiana, between 1953 and 2005, probably as a result of human development of the shoreline (O'Connell et al. 2007). In Mexico, decline is attributed to urban and agricultural expansion and dams (Mendoza et al. 2002).

Overharvest appears to play a role in the decline of Alligator Gars and Tropical Gars in some areas. Contributing factors for Alligator Gars include the long time required to reach maturity (see ecology section) and susceptibility to harvest by commercial and recreational fishers (Ferrara 2001; Brinkman 2008). Overharvest for food occurs in parts of Mexico and Central America. The harvest of Alligator Gars in Tamaulipas, Mexico, declined by 56% from 1988 (13.2 m^3) to 1990 (5.7 m^3) and by 80% between 1990 and 1997 (1.1 m^3). This led to a government program of captive rearing and release of larvae to supplement populations (Mendoza et al. 2002). Similarly, the harvest of Tropical Gars in the state of Tabasco, Mexico, declined from 481 mt in 1996 to 199 mt in 1999, possibly as a result of overharvest, but with only two points in time, it is not clear that this represents a trend of decline (Aguilera et al. 2002).

COMMERCIAL IMPORTANCE

Some Gars are sold in the aquarium trade, their parts have been and are used for various functions, and they sometimes constitute commercial and recreational fisheries. The Florida Gar has an attractive color pattern and its relatively small adult size makes it a popular aquarium fish, except in community tanks where it eats most any fish smaller than it is. Longnose Gars, Spotted Gars, and Alligator Gars also occasionally turn up in the pet trade. The ganoid scales were once used by Native Americans as arrowheads (Scarnecchia 1992), the skin was used as decorative covering for "picture frames, purses, and fancy boxes" (Forbes & Richardson 1920:34), and artisans often use the scales for jewelry and other forms of ornamentation (Mendoza et al. 2010a). Gars are a significant component of recreational fishing in some areas of the United States, Mexico, and Costa Rica (Ferrara 2001; Mendoza et al. 2010a). The large size and shallow-water habits of Alligator Gars make them particularly attractive to bow-hunters and trophy fishers (Brinkman 2008).

The meat of Gars, although well-flavored and good when baked, smoked, or fried (Becker 1983), generally is not commercially desirable in the United States, except in some areas of the southeastern United States (Suttkus 1963; Ferrara 2001). The commercial harvest of Alligator Gars averaged 237,509 kg/year from 1999 through 2006 in Louisiana (DiBenedetto 2009) and 368,846 kg/year from 1975 to 1985 in Arkansas (Robison & Buchanan 1988). Local harvest of Alligator Gars and Tropical Gars is a significant food source in parts of northeastern Mexico and Meso-America, respectively (Suttkus 1963; Mendoza et al. 2010a). For example, Tropical Gars in Lake Nicaragua were dried and sold locally or shipped to Guatemala City in the 1970s (Davies 1976), and the species "is a common part of the human diet in the area of Tabasco, Mexico, where it is one of the five main fishes traditionally consumed" (Barrientos-Villalobos & Espinosa de Los Monteros 2008:1920). Alligator Gars are commonly harvested for meat in Tamaulipas, Mexico, where they are "highly appreciated for their size and the quality of their meat" (Mendoza et al. 2002:134).

LITERATURE GUIDE

Grande (2010) described the history of conflict and reconciliation between morphology and molecular genetics regarding relationships among the basal actinopterygians, including Gars, along with monographic treatment of morphology (primarily skeletal) and its phylogenetic interpretation for all presently recognized living and extinct Gars. The detailed osteology of Gars is addressed in several papers (Mayhew 1924; Goodrich 1930; Suttkus 1963; Patterson 1973; Wiley 1976; Jollie 1984) and Grande (2010) covers it extensively. Grande's (2010) and Wiley's (1976) earlier monographs treat the biogeography of Gars. The edited volume by Mendoza et al. (2010b) reviews a great deal of Gar biology with an emphasis on captive culture. Spitzer's (2010) book presents a light-hearted, well-documented critique of the myths (large Gars are to be feared; Gars are destructive of the fishery) and misperceptions (Gars are foul and bad-tasting) behind the anti-Gar attitudes held by many fishers and until recent decades by many fishery managers. It includes an impassioned and compelling argument for preservation of Gars, particularly the Alligator Gar. Both Mendoza et al. (2010b) and Spitzer (2010) present recipes for the preparation and cooking of Gars.

Acknowledgments

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Chapter 8 Amiidae: Bowfins

Brooks M. Burr and Micah G. Bennett

The family Amiidae, the Bowfins, has only one living species, the North American Bowfin (*Amia calva*), although numerous (about nine genera) fossil Bowfins date back to Early Cretaceous times (118 mya). Originally described by Linnaeus (1766) from a specimen sent to him from Charleston, South Carolina, this morphologically distinctive fish has ≥11 recognized synonyms (Jordan & Evermann 1896; Eschmeyer & Fricke 2011). The species reaches a size of 109 cm TL (43 inches) and 9.8 kg (21.5 pounds). The origin of the genus name (*Amia*) is somewhat enigmatic but is apparently an old name for some kind of fish, possibly the Atlantic Bonito (*Sarda sarda*) (Jordan & Evermann 1896); "amia" is a Greek word meaning tunny (i.e., Tunas, Mackerels, Bonitos). The Bowfin has almost no resemblance to any member of the Scombridae (Mackerels and Tunas) (Fig. 8.1). "Calva" means bald or smooth, probably in reference to the scaleless head. The common name Bowfin derives from the long dorsal fin that undulates in ribbon-like (bow-like) waves. The Bowfin also goes by many other vernacular names (e.g., dogfish, mudfish, grindle, grunnel, lake lawyer, cypress trout, choupique [in Cajun French], and shoepick [in American English]), but its common name has been stable in the academic community for more than a century. The Bowfin is an effective predator in lowland streams, rivers, oxbow and glacial lakes, ponds, ditches, sloughs, and swamps where there is abundant cover (e.g., submerged logs, fallen timber, submerged vegetation). Sharp teeth and an ambush behavior usually result in prey being impaled on the teeth and swallowed whole (Fig. 8.2). One of the most unusual aspects of the natural history of the Bowfin is that among our few ancient fish lineages (i.e., Paddlefishes, Polyodontidae; Sturgeons, Acipenseridae; Gars, Lepisosteidae), it is the only nest-building species that also provides extensive parental care to its young (Reighard 1903). Bowfin populations are considered stable over much of their range, probably because they do not have to migrate long distances to spawn, are perceived to be of only moderate commercial value, and can survive hypoxic water conditions. Bowfin eggs are processed into caviar in some southern states (e.g., Louisiana), and the skull and skeleton are used in almost every comparative vertebrate anatomy class taught in the United States. No ichthyology student ever forgets her or his first view of the striking blue-green spawning colors of a male caught in the spring.

DIVERSITY AND DISTRIBUTION

The family Amiidae is restricted to eastern North America and consists of only one extant species. The Bowfin (*Amia calva*) is a strictly freshwater species that is native to the St. Lawrence, Great Lakes, and Mississippi River basins from Quebec to northern Minnesota and south to the Gulf Coast and on the Atlantic and Gulf coastal plains from the Susquehanna River drainage, southeastern Pennsylvania, to the Colorado River, Texas (Fig. 8.3). The Bowfin is still present in all the states and provinces from which it was originally recorded and is considered locally common. Introductions outside of North America are unknown.

Inter- and Intraspecific Variation

Although the Bowfin was described as new 12 times, all of the names date to the 19th century, and none are considered to represent a valid species (i.e., all are synonyms of *Amia calva*). In the Kissimmee River drainage, Florida, Bowfin

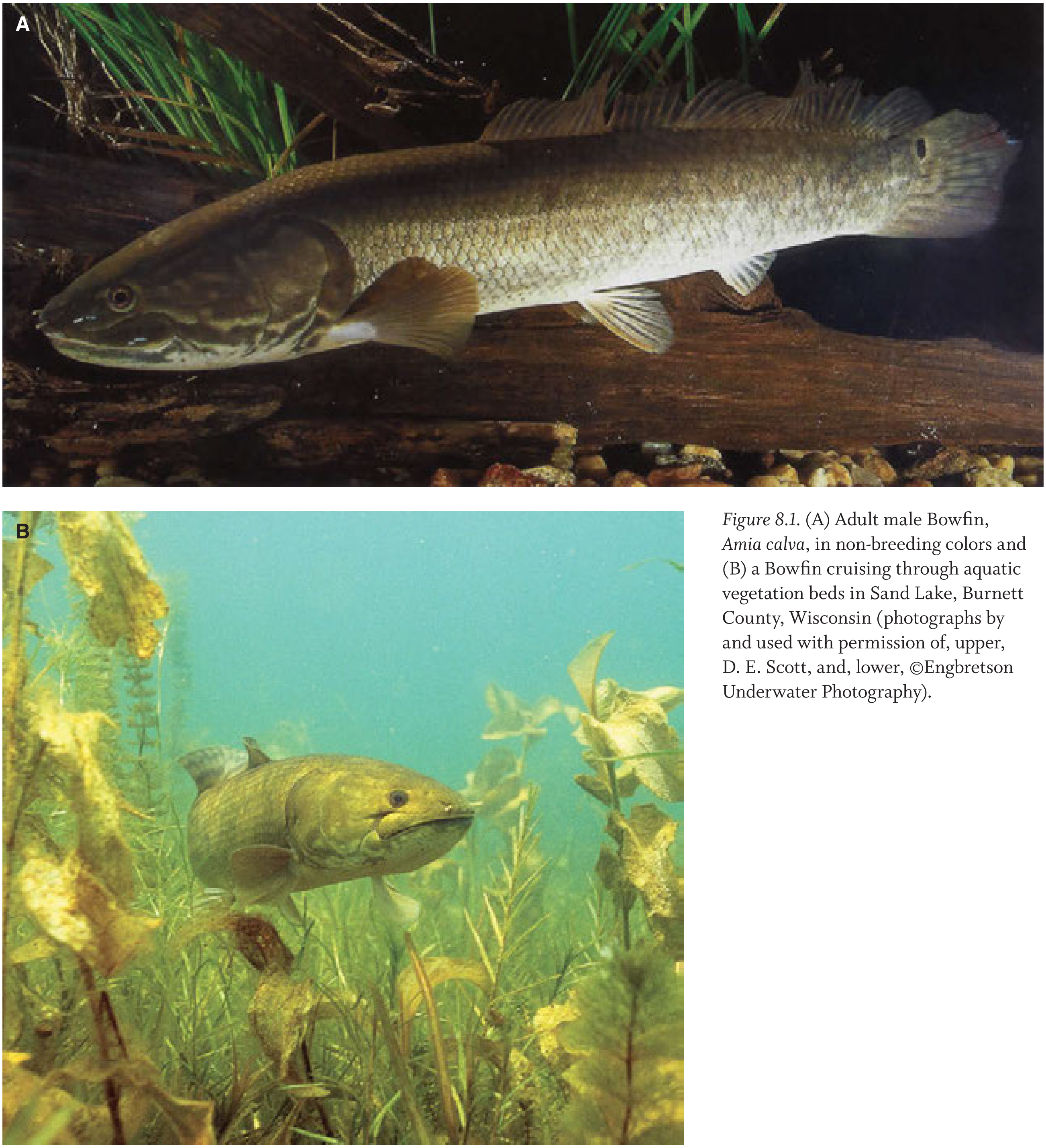


Figure 8.1. (A) Adult male Bowfin, *Amia calva*, in non-breeding colors and (B) a Bowfin cruising through aquatic vegetation beds in Sand Lake, Burnett County, Wisconsin (photographs by and used with permission of, upper, D. E. Scott, and, lower, ©Engbretson Underwater Photography).

were described as uniformly greenish-gray on the dorsum with no reticulated pattern or markings of any kind (Funderburg & Gilbert 1963). The venter was white or yellowish-white, and the black spot at the base of the caudal fin was lacking in both sexes with no ocellus in the male. Those from the Peace River, Florida, were similar but had a faint black spot on the caudal fin. No further descriptive work is available on these populations, and their status remains unstudied. Analysis of 75 Bowfin sampled from South Carolina to Louisiana and subjected to restriction fragment length polymorphisms in mitochondrial DNA showed two distinctive populations: (1) the eastern population extends from South Carolina to and including the Apalachicola River; (2) the western population is found from the Escambia River to central Mississippi (Bermingham & Avise 1986). Several other fishes showed a similar zoogeographic pattern in this region.

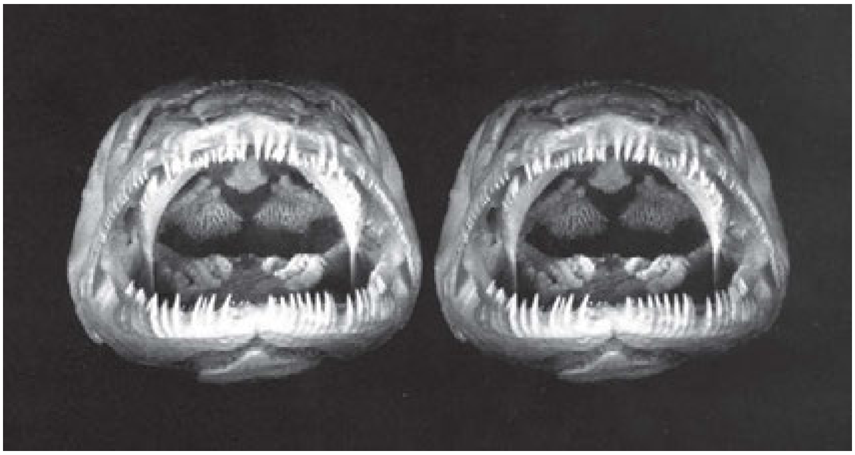


Figure 8.2. Stereograph of the Bowfin, *Amia calva* (450 mm SL). Anterior view looking into the open mouth of an adult dried skull showing the positions of the many teeth in the jaws, branchial arches, and palatal region (from Grande & Bemis 1998; used with permission of L. Grande).

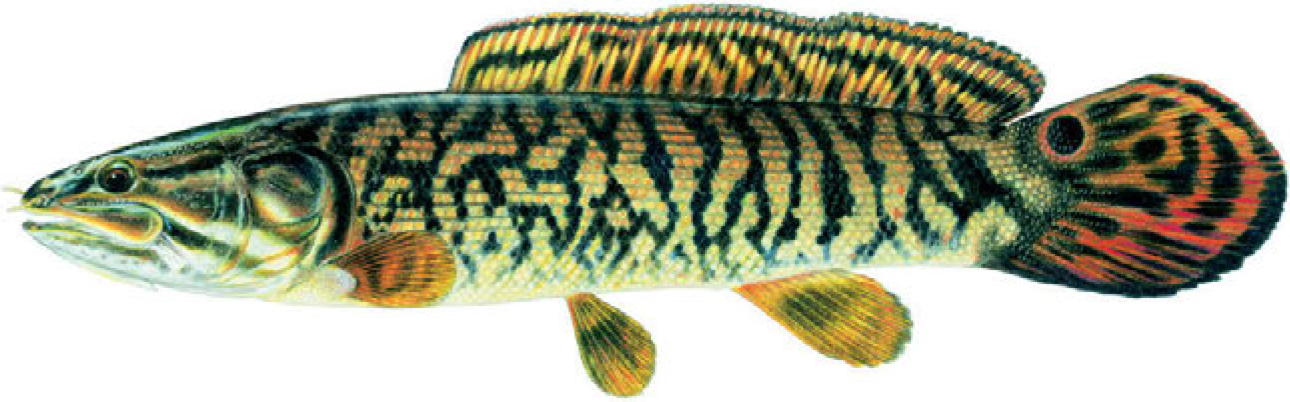


Plate 8.1. Bowfin, *Amia calva*

Bowfin as a Non-Native

Bowfin have likely been introduced widely across the United States, although whether specific population occurrences are native or introduced is debated (Pearson & Ward 1972; Denoncourt et al. 1975; Lee et al. 1980; Becker 1983; Jenkins & Burkhead 1994; Cross & Collins 1995; Mills et al. 1996; Pflieger 1997). In a review, Fuller et al. (1999) listed 15 states with evidence of introduction of the Bowfin. Records from the Missouri River drainage in Missouri and a single record from Kansas are attributable to escapees from stocked private lakes (Pflieger 1997), but the escapees apparently did not establish reproducing populations. Even so, intentional stocking of private lakes and ponds with subsequent flooding and overflow (Pflieger 1997) sometimes leads to dispersal, establishment, and range expansion (e.g., Pearson & Ward 1972). Other introductions were part of intentional state stocking programs (e.g., Pennsylvania, Denoncourt et al. 1975; Jenkins & Burkhead 1994) or were accidental (Cross & Collins 1995). Although the impacts of these introductions are undocumented, the opportunistic and predatory foraging of Bowfin suggests that as non-natives they may pose a threat to native fishes and other aquatic organisms (Fuller et al. 1999).

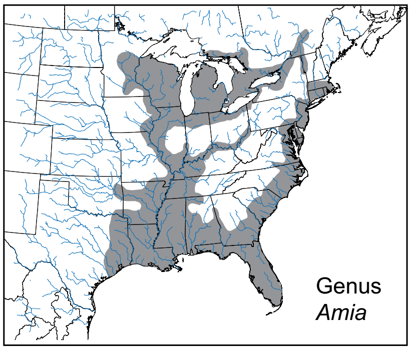


Figure 8.3. Geographic range of the Bowfin, *Amia calva*, the only extant representative of the Amiidae.

PHYLOGENETIC RELATIONSHIPS

With only 1 living species and nearly 30 extinct ones, the phylogenetic relationships of Amiidae and its relationships

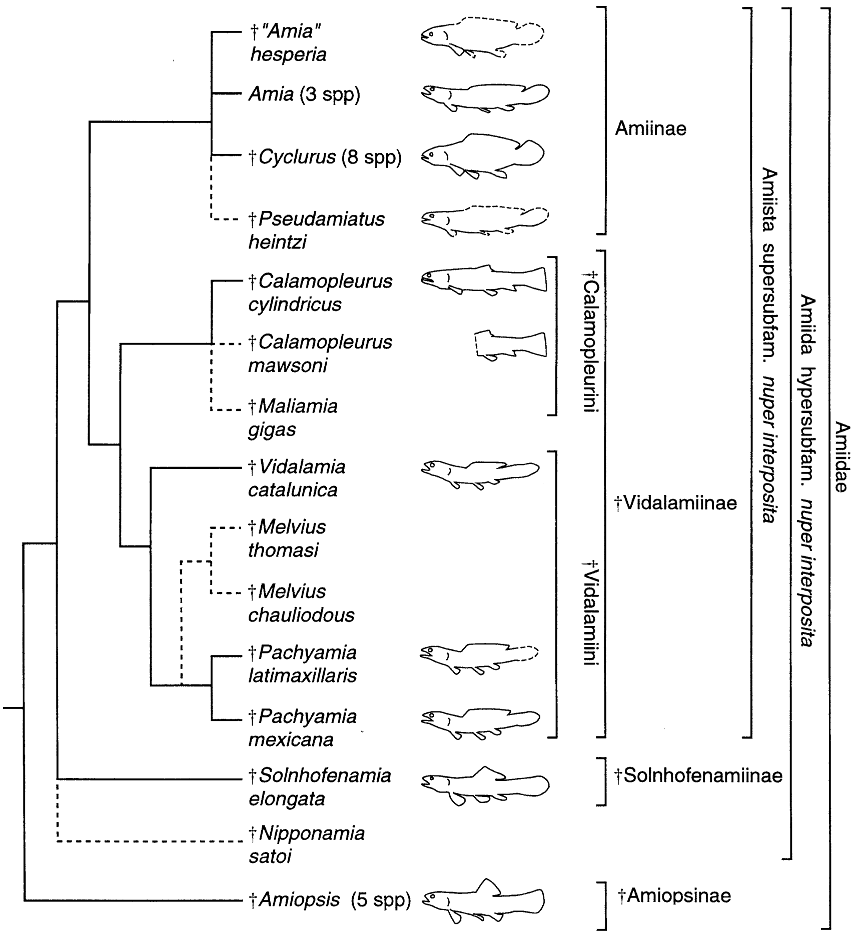

†"Amia" hesperia
Amia (3 spp)
†Cyclurus (8 spp)
†Pseudamiatus heintzi
†Calamopleurus cylindricus
†Calamopleurus mawsoni
†Maliamia gigas
†Vidalamia catalunica
†Melvius thomasi
†Melvius chauliodous
†Pachyamia latimaxillaris
†Pachyamia mexicana
†Solnhofenamia elongata
†Nipponamia satoi
†Amiopsis (5 spp)
Amiinae
†Calamopleurini
†Vidalamiini
†Vidalamiinae
†Solnhofenamiinae
†Amiopsinae
Amiista supersubfam. nuper interposita
Amiida hypersubfam. nuper interposita
Amiidae

Figure 8.4. Phylogeny of the family Amiidae based on morphology. Some taxa (dashed lines), often because of incomplete fossil material, were inserted into the phylogeny based largely on the authors' interpretation of certain characters (modified from Grande & Bemis 1998; used with permission of L. Grande).

to Actinopterygii (Ray-finned Fishes) are, out of necessity, based almost exclusively on morphological characters. Grande & Bemis (1998) incorporated all known fossils in their phylogenetic treatment (Fig. 8.4), which shows the genus †*Amiopsis* as basal to the family. The subfamily †Vidalamiinae is the sister-group to Amiinae; †Solnhofenamiinae is the sister-group to those two subfamilies. Some taxa, often because of incomplete material, were inserted into the phylogeny based largely on the authors' interpretation of certain characters. They considered amiids as part of a larger clade (all extinct taxa) to make up a monophyletic Halecomorphi (Grande & Bemis 1998). In this sense, the †Sinamiidae are sister to Amiidae, and the †Caturoidea are sister to those two families; these three taxa make up the order Amiiformes. The Halecomorphi are then sister to Teleostei that together make up the Halecostomi. Some earlier works largely supported these conclusions, but the latter findings based on morphology have brought us back to the earlier outcome that Amiidae is sister to Lepisosteidae (Gars), and these two families (and orders) should be placed back into a monophyletic Holostei (Grande 2005; Grande 2010). The issues and ultimate phylogenetic relationships of Amiidae-Lepisosteidae-Telesotei are complicated because of several poorly studied fossil groups that may be relevant to the central questions of monophyly and teleost phylogeny.

One fossil taxon (detailed by Grande 2010) helped overturn a phylogenetic pattern derived from the morphology of extant species. The Cretaceous family, †Obaichthyidae, known from Morocco and Brazil, is a diagnosable group related to extant Gars; specimens have a well-developed interopercle and other features that falsify previously proposed shared-derived characters for the monophyly of Halecostomi. Improved preparation of the fossils in question showed that these characters were missed in previous descriptions of †*Obaichthys* and help unite a monophyletic Holostei. Grande (2010:1) stated that †Obaichthyidae "represent a phylogenetic 'missing link' in the truest sense of the term." Grande's conclusions also are supported by molecular studies that have examined extant *Amia*, Lepisosteidae, and Teleostei in numerous phylogenetic analyses (Normark et al. 1991; Le et al. 1993; Venkatesh et al.

2001; Inoue et al. 2003; Kikugawa et al. 2004). In brief, a monophyletic Holostei is once again the sister-group of Teleostei (Fig. 8.5).

FOSSIL RECORD

In a comprehensive study of amiid fishes, Grande & Bemis (1998) classified the family into four subfamilies: Amiinae (including the genera *Amia*, †*Cyclurus*, †*Pseudamiatus*, and †*"Amia" hesperia*), †Vidalamiinae (including the genera †*Vidalamia*, †*Pachyamia*, †*Melvius*, †*Calamopleurus*, and †*Maliama*), †Solnhofenamiinae (including the genus †*Solnhofenamia*), and †Amiopsinae (including the genus †*Amiopsis*). Numerous (>30) other taxa thought to be related to Amiidae were studied and rejected because the material lacked the diagnosable traits of the family. Amiinae is the only subfamily to have survived beyond the Early Eocene (about 48.6 mya). The Amiinae was a diverse clade with a stratigraphic range of Late Cretaceous (about 99.6–65.5 mya) to the present. There are three diagnosable species of extinct *Amia* and eight of †*Cyclurus*. The third genus in the subfamily, †*Pseudamiatus*, is an incompletely prepared specimen and might actually belong in *Amia* or †*Cyclurus*. All of these extinct genera were apparently confined to fresh waters and were especially speciose during the Eocene (55.8–33.9 mya). The materials on which Grande & Bemis (1998) based their conclusions represent well-preserved and often complete specimens (Fig. 8.6).

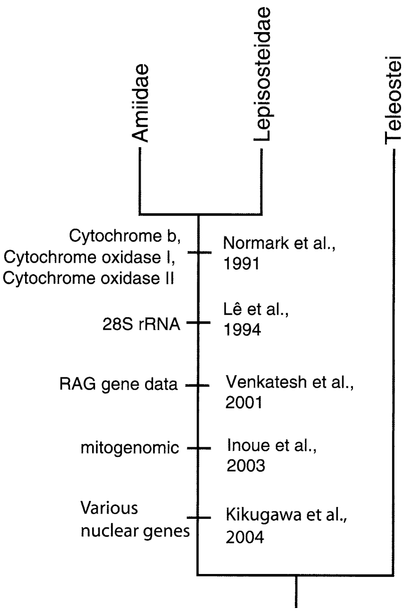


Figure 8.5. Relationships of the Neopterygii based on molecular data sets. Note that all of the studies demonstrate a monophyletic Holostei (from Grande 2010; used with permission of L. Grande).

Fossil species of Amiinae extend the geographic range of the living species to western North America, Europe, and Asia. Nearly complete skeletons are known from Wyoming and Colorado (Grande & Bemis 1998); †*"Amia" hesperia* was found in British Columbia. Amiines were among the world's most widespread freshwater fishes during the Early Tertiary. Almost every Paleocene (65.5–61.7 mya) or Eocene freshwater deposit containing vertebrate fossils (particularly in western North America) includes at least a few amiine fragments (Grande & Bemis 1998).

The †Vidalamiinae, the sister-group to Amiinae, is a diverse group (11 species) with some species reaching nearly 2 m TL (6.6 feet) that is known only from the Early Cretaceous (145.5–99.6 mya) to the Early Eocene (55.8–48.6 mya). Species are known from Spain, the Middle East, southern Mexico, Brazil, Morocco, and east-central Africa. Those for which the paleoenvironments are known come primarily from marine or brackish deposits (Fig. 8.7).

A fossilized maxilla of an amiid (placed in †Vidalamiini *incertae sedis*) from the Eocene of Senegal is considered to be from a shallow marine deposit (O'Leary et al. 2012). The significance of this discovery is in the occurrence of an amiid in marine rocks after the Cretaceous-Paleogene time period because this contradicts the existing hypothesis that marine amiids were generally absent (replaced by freshwater taxa) after this time boundary.

The other two subfamilies contain six diagnosable species and are Late Jurassic (161–145.5 mya) to Late Cretaceous in age. They occur in marine and freshwater deposits,

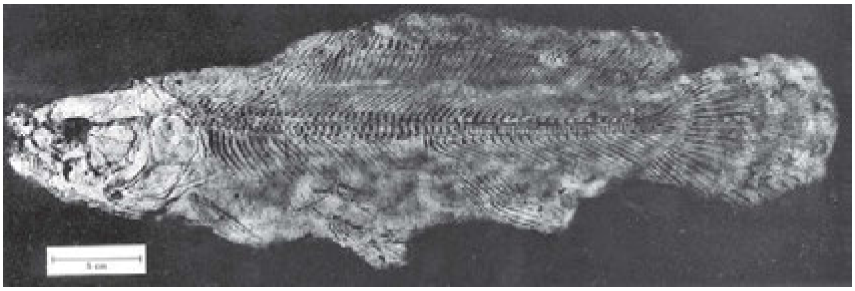
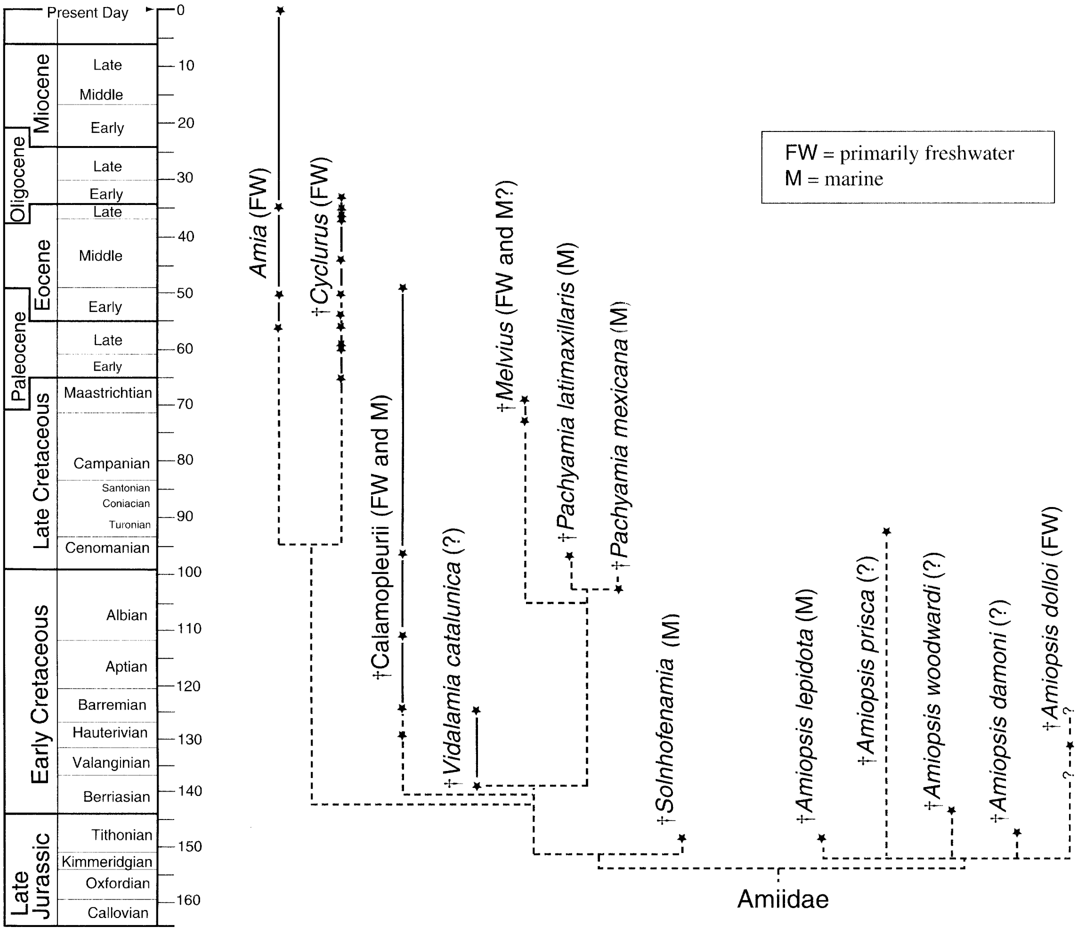


Figure 8.6. Lateral view of †*Amia scutata* (385 mm SL) showing well-preserved, nearly complete skeleton from Late Eocene (37.2–33.9 mya) freshwater deposits of Florissant Formation, Teller County, Colorado (from Grande & Bemis 1998; used with permission of L. Grande).


Present Day
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Eocene
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Paleocene
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Early
Late Cretaceous
Maastrichtian
Campanian
Santonian
Coniacian
Turonian
Cenomanian
Early Cretaceous
Albian
Aptian
Barremian
Hauterivian
Valanginian
Berriasian
Late Jurassic
Tithonian
Kimmeridgian
Oxfordian
Callovian
FW = primarily freshwater
M = marine
Amia (FW)
†Cyclurus (FW)
†Calamopleurii (FW and M)
†Vidalamia catalunica (?)
†Melvius (FW and M?)
†Pachyamia latimaxillaris (M)
†Pachyamia mexicana (M)
†Solnhofenamia (M)
†Amiopsis lepidota (M)
†Amiopsis prisca (?)
†Amiopsis woodwardi (?)
†Amiopsis damoni (?)
†Amiopsis dolloi (FW)
?
?
Amiidae

Figure 8.7. Paleoecological data and geological time ranges of amiid taxa. Stars are actual occurrence levels of diagnosable species described in Grande & Bemis (1998). Solid lines indicate known stratigraphic ranges. The scale is in millions of years ago (modified from Grande & Bemis 1998; used with permission of L. Grande).

and adequate study material comes from Germany, France, Spain, England, Yugoslavia, and Belgium. When other extinct taxa thought to be amiids (mostly fragmentary material) are plotted on an equal area projection map (Fig. 8.8), the family clearly was nearly worldwide in geographical distribution, missing only from the Australasian and Antarctic regions.

Most amiids apparently were piscivorous, and several specimens had other fishes preserved in their stomachs. The genus †*Cyclurus* may be an exception with some evidence to suggest a diet of mollusks or arthropods (Grande & Bemis 1998). Piscivory is probably a basal trait among Halecomorphi, and as such, the dietary habit of †*Cyclurus* was derived.

MORPHOLOGY

The extant Bowfin is a distinctive species characterized externally by a long, nearly cylindrical body; an abbreviate heterocercal caudal fin; a long dorsal fin (48–51 segmented rays) extending more than half the length of the back; tubular nostrils; a large bony gular plate on the throat (Fig. 8.9); rounded pectoral, pelvic, and caudal fins; and cycloid scales. Adults are usually mottled green on the back and sides with a cream yellow to pale green venter. Black bands are on dark green dorsal and caudal fins. A yellow to orange halo surrounds a prominent black spot near the base of the upper caudal fin rays in young Bowfin; the spot is less distinct in most adults and usually absent in adult females. A male in breeding colors has brilliant turquoise blue-green lips, throat, belly, and ventral fins (Grande & Bemis 1998; Nelson 2006; Page & Burr 2011). Both albino and melanistic individuals have been caught by anglers. Small juveniles ≤60 mm TL (2.4 inches) are strikingly colored with black and orange (Figs. 8.10 and 8.11). The longest specimen reported is 109 cm TL (43 inches) (Page & Burr 2011), and the greatest weight reported is 9.7 kg (21.4 pounds). Lateral-line scales number 62–70; anal fin rays, 9–12; pelvic fin rays, 7; pectoral fin rays, 16–18; and caudal rays, 25–28.

To distinguish *Amia calva* from its fossil relatives, Grande & Bemis (1998) listed 5 internal characters for adults: 8–11

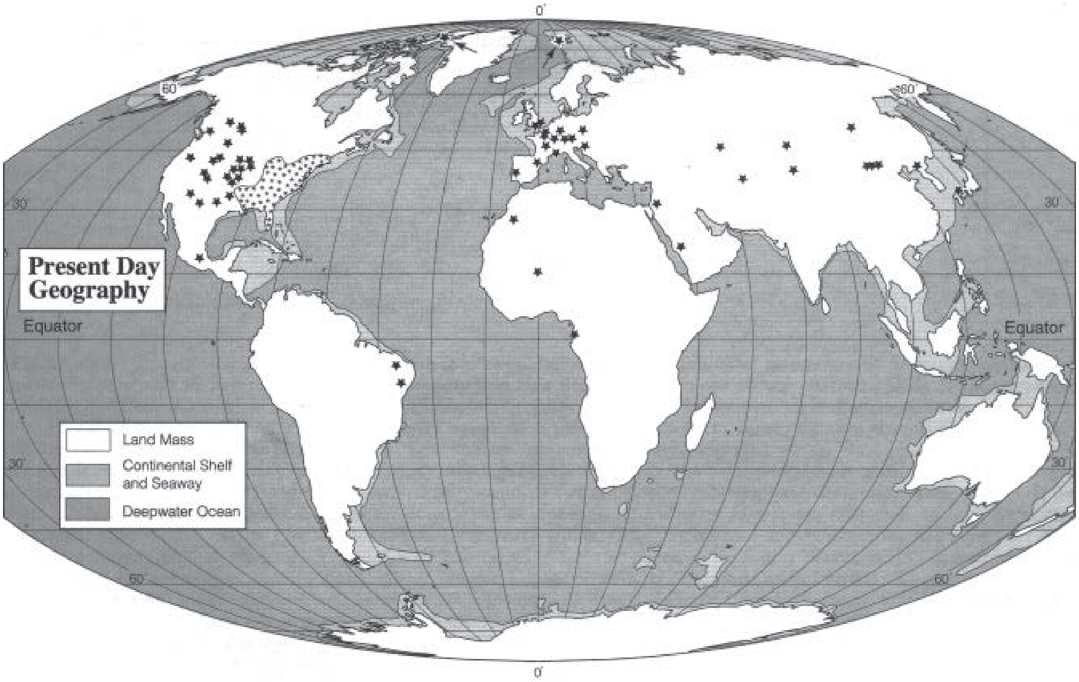

Figure 8.8. Geographic range of fossil and recent Amiidae. Small stars show general range of the Bowfin, *Amia calva*, the only extant species; large stars are fossil amiid localities (from Grande & Bemis 1998; used with permission of L. Grande).

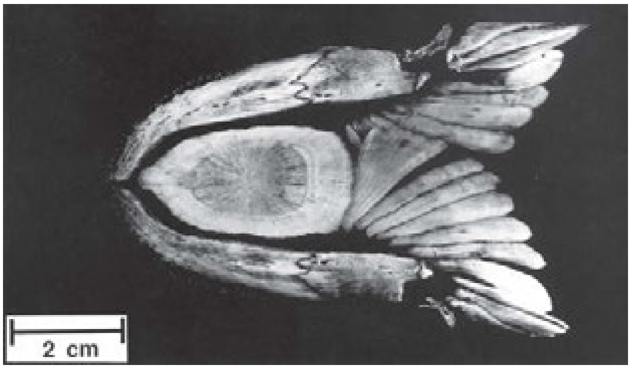

Figure 8.9. Ventral view of skull of the Bowfin, *Amia calva* (about 400 mm SL), showing gular plate shape and fusion of anterior branchiostegals (from Grande & Bemis 1998; used with permission of L. Grande).

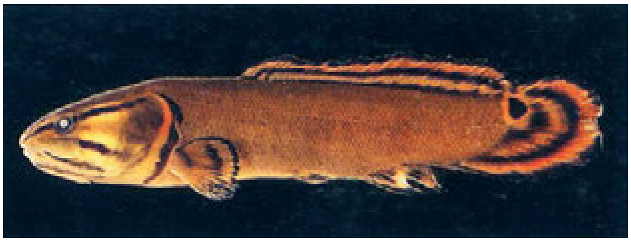

Figure 8.10. Juvenile (70 mm TL) of the Bowfin, *Amia calva*, showing orange and black colors, Altamaha River system, Georgia (photograph by and used with permission of Richard T. Bryant).

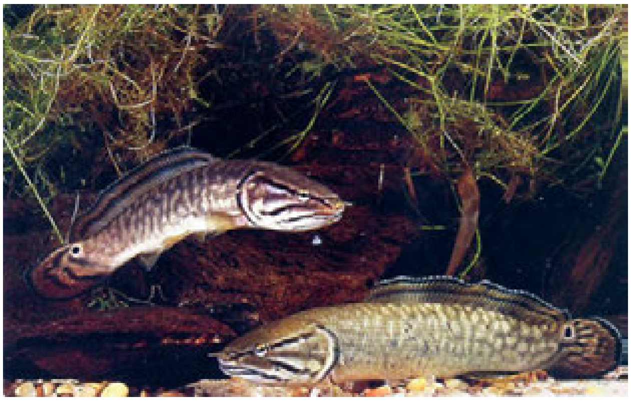

Figure 8.11. Two color forms of juvenile Bowfins, *Amia calva* (photograph by and used with permission of D. E. Scott).

supraneurals versus 6–8 in other amiine species; 48–51 segmented dorsal-fin rays versus either higher or lower counts for the other species of *Amia* (counts from >100 skeletons or cleared and stained specimens); 10 ural centra versus 7–9 in other species; 70–73 total vertebrae and 85–91 total centra versus 63–68 and 83–89 in others, respectively; and upper post-infraorbital bone as large or larger than the lower post-infraorbital. Unusually *Amia calva* has a highly vascularized and subdivided swim bladder that can be used as a lung (see physiology section); no pyloric caeca (Nelson 2006); and kidney tubules that open directly into the body cavity, a characteristic shared with Gars (Becker 1983).

Grande & Bemis (1998) treat the entire skull and skeleton of >100 specimens of *Amia calva* in magnificent detail with photographs, ink drawings, and descriptions of every bone. Remarkable variations occur in some skull roofing bones (e.g., frontal bones paired in most specimens, but one had only a single frontal bone). Adults usually have 4–5 coronoid teeth, 12–16 dentary teeth, 7–8 premaxillary teeth, and 14–49 maxillary teeth. The occipital condyle is formed by 11–14 branchiostegal rays and 1–2 fused vertebrae. A perusal of literature on Bowfin characters showed more variability in dorsal-fin ray numbers than any other meristic feature (some counts as low as 42 rays, Marcy et al. 2005).

GENETICS

Karyology

Bowfin have a karyotype of 46 chromosomes with 10 metacentric and 13 acrocentric pairs and, unlike Gars, no microchromosomes (Ohno et al. 1969). Although genomes of non-teleost fishes like Bowfin are as yet unsequenced, current hypotheses suggest a high amount of chromosomal fusion during the transition from an osteichthyan ancestor to the evolution of actinopterygians (Sato & Nishida 2010).

Genome Size and Variation

Early estimates of Bowfin mitochondrial genome size ranged from 16,000–16,900 base pairs (bp) (Bermingham et al. 1986), which is concordant with later complete sequences (Inoue et al. 2003). Basal actinopterygians like the Bowfin share with most vertebrates an intact cluster of ParaHox genes, a group of three genes that arose at least as early as Bilateria, and which are important in multiple developmental pathways. Teleosts, however, lost this cluster after multiple genome duplication events, indicating that the selective pressures that maintained the cluster were relaxed during teleost evolution (Mulley et al. 2006; Sato & Nishida 2010). Many different sequences (>100) of mitochondrial and nuclear genes and fragments are sequenced and available for use on GenBank (National Center for Biotechnology Information 2011).

Intraspecific Genetic Variation and Phylogeography

Analysis of mtDNA fragments of Bowfin from 20 localities in 13 major drainages of the southeastern United States revealed 13 different clones and 2 main genotypic clusters: one east of and including the Apalachicola River and one west of the Apalachicola River. These clades differed by about 1% sequence divergence. Within the eastern clade, samples from the Everglades and the St. Johns and Suwanee Rivers formed an additional clade. Clones within the eastern group occurred in multiple eastern drainages, but clones in the western group were restricted to single drainages (Bermingham & Avise 1986; Avise et al. 1987; Avise 1992). This break between eastern and western populations appears to be a common feature of phylogeographic studies of aquatic and terrestrial organisms in the southeastern United States with the exact location of the break varying but usually occurring in the Florida panhandle (Bermingham & Avise 1986; Avise et al. 1987; Avise 1992; Soltis et al. 2006).

PHYSIOLOGY

Bowfin are frequently used as model organisms for studying vertebrate evolution. As such they are the subject of many studies on the structure, function, and development of hormones (e.g., Amemiya & Youson 2004), enzymes (e.g., Gilmour & Perry 2004), peptides and proteins (e.g., Wang & Conlon 1994, 1995; Wang et al. 1993), cellular and tissue structures and processes (e.g. Youson et al. 2001), and other aspects of metabolism, physiology, and neurobiology that, although examined, are not used in the synthesis here. We focus here on respiration, tolerances to environmental extremes, vision, the acousticolateralis system, olfaction and chemosensation, and digestion.

Oxygen Requirements, Respiration, and Air Breathing

Under certain conditions, Bowfin are facultative air breathers, taking in oxygen from the air through a highly vascularized swim bladder or lung (Daxboeck et al. 1981; McKenzie et al. 1991a). Bowfin increase air-breathing activity during exercise, in low-pH conditions, and with increasing temperatures (at 30°C, 86°F, air breathing increased threefold) (Johansen et al. 1970; Horn & Riggs 1973; Farmer & Jackson 1998), but detailed experiments indicated that increased air breathing occurs in response to decreases in blood oxygen concentration not increased carbon dioxide pressure or pH level in the blood (McKenzie et al. 1991ab). Environmental hypoxia reduces the ability of the gills to maximize oxygen pressure in the arteries and triggers air-breathing activity through chemoreceptors. At one time, researchers concluded that these chemoreceptors were located peripherally (as opposed to part of the brain, brainstem, or other part of the central nervous system [CNS]) (Hedrick et al. 1991; Katz 1996); however, experimental results from Longnose Gar were consistent with central neuronal chemoreception of low pH and CNS control of air-breathing activity, the first evidence of CNS chemoreception in an ancient actinopterygian (Wilson et al. 2000). Although unconfirmed, neuroendocrine cells in the gills are also implicated as playing a role in hypoxia sensation and regulation of air breathing and blood chemistry (Goniakowska-Witalinska et al. 1995).

Like other air-breathing actinopterygians, Bowfin have a four-phase process for aerating the air bladder: (1) the buccal cavity expands and fills with expired air; (2) the buccal cavity compresses, expelling expired air; (3) the buccal cavity expands again to take in fresh air; (4) the buccal cavity contracts again, forcing fresh air into the bladder (Brainerd 1994, 1997). Bowfin air-breathing behavior is classified into two types: exhalation-inhalation (Type I), triggered by low environmental oxygen conditions and regulating gas exchange, and inhalation-only (Type II), regulating air-bladder size and buoyancy and triggered by receptors detecting bladder volume (Milsom & Jones 1985; Hedrick & Jones 1993; Hedrick & Jones 1999). Type II air breathing exhibits a defined periodicity of about 30 min (Hedrick et al. 1994). Air breathing occurs more frequently at night than during the day (Horn & Riggs 1973). Bowfin blood has a relatively low oxygen affinity but exhibits a significant Bohr effect (a lowered affinity for oxygen by hemoglobin at lower pH) (Johansen et al. 1970; Randall et al. 1981), and a large Root effect (a decreased capacity of hemoglobin to bind oxygen at lower pH) (38–60% maximal hemoglobin O_2 desaturation) (Weber et al. 1976; Berenbrink et al. 2005; Regan & Brauner 2010a). Even so, early experiments found only 10% reduction in hemoglobin oxygen capacity with 0.8 reduction in pH (Johansen et al. 1970). In a spring in Florida, Bowfin occurred in waters with 2.3–3.6 ppm dissolved oxygen (Odum & Caldwell 1955), but the species regularly occurs in densely vegetated waters in the southern United States with dissolved oxygen levels <1 ppm (Killgore & Hoover 2001) and has the highest tolerance indicator value for freshwater fish tolerance to hypoxic conditions (Meador & Carlyle 2007 and supplemental data). The habit of surfacing for atmospheric air is ordinarily discontinued in cold weather, except under conditions of low oxygen. Under these conditions, Pflieger (1997:61) “once observed a group of Bowfins surfacing so frequently that they maintained an area of open water in a lake that was otherwise completely frozen over.”

Salinity Tolerance

Among freshwater fishes, Bowfin easily tolerate relatively high natural salinity levels in brackish marshes and estuaries (1.6–5.0 ppt; Pearson & Ward 1972). The species can also survive under much higher values (16–18 ppt) with a lethal limit likely around 19–20 ppt (Chipman 1959). Young-of-the-year Bowfin survived well in 24% sea water (about 8.4 ppt) but died in 30% sea water (about 10.5 ppt) (Hanson et al. 1976). Juvenile Bowfin transferred to 20–24% sea water had elevated blood cortisol levels for 7–8 days after transfer, indicating a potential role for this stress hormone in physiological adaptation to high-salinity environments (Hanson & Fleming 1979).

Thermal Capacity and Preferred Temperature

Preferred temperature (24 h) averages 30.5°C (86.9°F) with a diurnal mean of 31.3°C (88.3°F) and a nocturnal mean of 29.6°C (85.3°F) (Reynolds et al. 1978). The critical thermal maximum for Bowfin is near 35.2°C (95.4°F) (Horn & Riggs 1973). Juvenile Bowfin transferred to ice water (0°C, 32°F) for 120 s showed increased levels of the stress hormone cortisol in the blood, but this lasted <30 min (Hanson & Fleming 1979).

Acidity Tolerance

Bowfin exposed to low-pH waters experience high acidity in body fluids, tissues, and cells (acidosis) that if prolonged can cause tissue damage and death (Wood et al. 1983). Bowfin increase air-breathing activity during low-pH conditions (McKenzie et al. 1991a), but their main site for acidic carbon dioxide excretion is the gills (Randall et al. 1981). Thus, though increasing oxygen absorption, air breathing may actually hinder pH balancing. Experiments show that the cause of low-pH conditions (environmental or exercise and movement) impacts whether air breathing aids or hinders acidosis recovery. Fish that underwent vigorous exercise (and thus had low body pH) and were allowed to breathe air recovered to pre-exercise pH levels more slowly (>8 h) than those without access to air (4–8 h) due to their decreased ability to excrete carbon dioxide and hydrogen ions (H^+) across the gills. Fish exposed to low-pH (3.5) water and allowed to breathe air, however, had milder acidosis than those with no air access. This was due to increased lactic acid production in fish without air access. Under these circumstances, increased oxygen uptake from air breathing prevented anaerobic metabolism and lactic acid production and also prevented the loss of plasma ions (Na^+ and Cl^-) normally associated with low-pH conditions (Gonzalez et al. 2001).

Stress

Bowfin exhibit small but significant responses to handling and transport with plasma corticosteroid levels after 2 h of transportation increasing an average of 3 times (14 ng/mL) above levels just after being electroshocked (Davis & Parker 1986). As mentioned, Bowfin show stress responses to high salinity and cold temperatures (Hanson & Fleming 1979).

Survival in Extreme Environments

Early naturalists suggested that Bowfin enter aestivation, a period of decreased metabolism when exposed to conditions requiring prolonged air breathing, if trapped by lowering water levels. One observer found an adult Bowfin in a spherical chamber about 10 cm (4 inches) from the ground surface after hearing it writhing about. The surface of the ground was dry and permanent water was almost 0.4 km (0.25 mile) away but prior flooding was evident and the interior of the chamber (20 cm diameter, 8 inches) was moist (Neill 1950). In Louisiana, Bowfin were also reportedly plowed up from lowland agricultural fields weeks after water levels had dropped enough for cultivation (Gowanloch 1933). More recent laboratory work showed that the Bowfin does not truly aestivate because it does not detoxify ammonia by converting it to urea and does not reduce metabolism in response to hypoxia, both characteristics of true aestivation (e.g., African Lungfishes, Protopteridae) (McKenzie & Randall 1990). Regardless of the lack of evidence for aestivation, Bowfin can survive prolonged conditions of exposure to air due to their ability to breathe air and the rigid structure of their gill filaments and lamellae that helps prevent collapse of the lamellae and aids gas exchange even during air exposure (Bevelander 1934; Daxobeck et al. 1981). The species was found in shallow puddles of mud and water left behind weeks after flood waters receded (Gowanloch 1933). Young Bowfin (mean 406 mm, 16 inches) survived in a drained pond for 21 days in only slightly moist mud (Green 1966), and adults kept out of water can survive 24 h without evidence of damage (Eddy & Underhill 1974) and 3–5 days before death (McKenzie & Randall 1990).

Vision, Photoreceptors, and Visual Pigments

Bowfin retina contain a nearly equal ratio of rods (low light–sensitive photoreceptors) to single and double cones (photoreceptors responsible for vision in bright light), and this varies little with retinal region. In many teleosts, low-light conditions cause the cones to retract from their position near the external retinal membrane to make room for the large numbers of rods; however, in the Bowfin retina, the relatively low rod:cone ratio compared with other fishes makes cone movement largely unnecessary (Ali & Anctil 1974). Consequently, a study of the electroretinograms (ERGs) of Bowfin revealed lower amplitudes of the b-wave (~80–120 μV), indicating lower retinal sensitivity, than Atlantic Salmon (*Salmo salar*) (206–340 μV), both overall and in the dark. Bowfin ERGs also exhibited slower responses (higher latency) of all waves (a: ~18–20 msec; b: ~40–55 msec; c: ~40–42 msec) in comparison with *S. salar* (a: ~15–17 msec; b: ~25–49 msec; c: ~18–19 msec). Bowfin had lower maximum fusion frequency (maximal rate at which wave stimuli can be perceived as separate, i.e., lines in ERG are not merged) in light (~38 cycles/s, cps) compared with the Atlantic Salmon (~88 cps); Pumpkinseed, *Lepomis gibbosus* (~80 cps), Brook Trout, *Salvelinus fontinalis* (~65 cps), and Goldfish, *Carassius auratus* (~55 cps). In the dark differences may be less (*S. fontinalis*, ~21 cps; *A. calva*, ~20 cps), but data are sparse. The authors related these differences among species to their habitats and activities, suggesting that the Bowfin is less dependent on vision and relies more on other sensory systems for its activities (Gramoni & Ali 1970).

Acousticolateralis System

As in most fishes, Bowfin sensation of sound, pressure, and orientation occurs through the acousticolateralis system. This system consists of the auditory and vestibular organs of the inner ear and sensory cells distributed along the lateral line and across the body that are responsible for mechanoreception (McCormick 1982). The auditory-vestibular portion of the system is composed of fluid-filled semicircular canals containing three main otoliths (inner ear bones): the saccule, the lagena, and the utricle. In Bowfin, the saccular and lagena epithelia are in a single chamber like in the Shovelnose Sturgeon (*Scaphirhynchus platorynchus*) and Bichirs (Polypteridae, genus *Polypterus*)

(Popper & Northcutt 1983; Manley & Clack 2004). Unlike in most teleosts, the lagena is larger than the saccule (Manley & Clack 2004) and takes precedence in terms of sensory region with >216,000 cells, followed by the utricle (>56,000 cells) and lagena (>8,600 cells) (Popper & Northcutt 1983). The otolith chambers are innervated by nerves connecting to lateral-line sensory pores that convey information on orientation, but other nerves from the lateral line connect to the central nervous system (McCormick 1981, 1982). The Bowfin, Gars, and Hagfishes (Myxinidae) are the only non-teleosts that lack the dorsal nucleus, a nexus of nerves responsible for electroreception, and thus species in these families cannot detect electric fields (Bullock et al. 1983).

Olfaction and Chemosensation

In Bowfin, the nasal opening is at the end of an extended tube, similar to that in Bichirs, and the olfactory organ itself is relatively near the anterior portion of the head as in most actinopterygians (e.g., Bichirs, lepisosteids). The olfactory rosette, the main site of olfaction, is made up of many folds of tissue, or lamellae, which can number >100 in Bowfin—much greater than in acipenserids (20–32), polyodontids (13–18), and lepisosteids (8–10). Secondary lamellae are absent (Chen & Arratia 1994).

Like most fishes, Bowfin taste buds contain two main cell types, electron-light and electron-dark, which form the epithelium of the taste bud and likely serve as secondary sensory cells. Within each of these cell types, Bowfin further exhibit two subtypes of taste bud microvilli (apical areas of taste bud cells that house the receptors). Although fishes from several diverse families exhibit variation in microvilli subtype in light cells, morphological variation in dark cell microvilli is much less frequent, and one of the subtypes appears unique to Bowfin. The significance of variation in taste bud microvilli subtype is unclear, but these appear to be species-specific and may have evolved as each species came to occupy a specific niche (Reutter et al. 2000; Reutter & Hansen 2005).

Digestion

Digestion rate in young-of-the-year Bowfin was slower than that of the Longnose Gar, *Lepisosteus osseus*, requiring 28–32 h to complete digestion of a food ration equaling 4.9% of body weight when held at a constant 21°C (69.8°F) (Herting & Witt 1968). An adult Bowfin had partially digested a large tadpole after 2.5 h, though the holding temperature was not given (Hopkins 1890). A Bowfin kept in captivity survived for 20 months without food (Smallwood 1916).

BEHAVIOR

The daily activities and behaviors of Bowfin are inadequately studied (but see reproduction section). Adults are mostly solitary and sedentary predators that spend considerable time in an almost motionless state. In winter, in Oconomowoc Lake, Wisconsin, Bowfin were "in schools closely huddled together in the bottom of pockets or shallow depressions of the gravelly bed of the lake, among the water-weeds . . . They lie so close together that occasionally two individuals are impaled on the fish-spear by one throw. When thus disturbed they scatter from their resting places. Moving out a short distance to return quickly after the first few disturbances" (Ayers in Reighard 1903:65). Observers have considered Bowfin in natural settings to be ambush predators. In swamps they can be heard hitting the surface of the water to presumably gulp air, and predation is often a crepuscular activity (Reighard 1903).

Movement and Dispersal

Little information is available on dispersal and movement in the Bowfin. Differences were not detected in diel motor activity (Reynolds et al. 1978), but no studies have examined longer-distance movements from day to night. Bowfin may move en masse into inundated floodplain habitat or tributaries during high-water periods, but this is likely associated with spawning activities (Eddy & Underhill 1974; Simon 1990). In the upper Mississippi River, Bowfin, along with other fishes like Northern Pike, *Esox lucius*, and crappies (*Pomoxis* spp.), actively moved out of backwater habitats toward the main channel with lowering water levels and current flow toward the main channel, unlike Bluegill and Largemouth Bass that tended to be trapped in isolated pools. In a Wisconsin study of fish movement under winter ice conditions between a backwater lake and the Mississippi River, >600 Bowfin were recorded in trap nets leaving the backwater and 206 individuals were detected entering the backwater; although all were marked, few individuals were recaptured (Greenbank 1956). Total fish movement, including Bowfin (January–February), was positively correlated with snow cover depth on the ice, and many more Bowfin entered the lake during this time than emigrated (Greenbank 1956). In the Savannah River, North Carolina, Bowfin migrate in spring from the river to lower portions of Steele Creek, returning to the river in autumn when the creek temperatures fall below that of the river (Marcy et al. 2005). Fish traps set over a 162-day period spanning 2 years revealed the Bowfin as one of the most abundant fishes (101 individuals, averaging 477 mm TL, 18.8 inches) moving from the Okefenokee Swamp through a spillway to the Suwannee River (Holder 1970). Via extrapolation of trap area to spillway area the author estimated about 6,400 Bowfin moved from the swamp to the river. Nearly all the movement occurred during December to February when water temperatures were at annual lows. Of 266 tagged Bowfin in a year-long study in a North Carolina swamp stream, only 35 were recaptured, and none of the recaptures had moved >0.2 km (0.12 mile) from the original tagging site (Whitehurst 1981).

Schooling

Yolk-sac larvae have a prominent adhesive organ on the snout that is used for attachment to plant materials. Once the yolk is absorbed the young school in a large black pod or swarm and are accompanied by the former nest-guarding male (Fig. 8.12). Most of the young in the pod usually swim at the same rate of speed, face the same direction, and move in concert (i.e., the school is polarized). Young remain with the adult male until about 100 mm TL (3.9 inches), but schools become smaller, more loosely aggregated, less polarized, and not well guarded after the young reach about 35 mm TL (1.4 inches). Brood protection then ends, and the young scatter to sheltered areas and begin to live and feed entirely on their own. In aquaria, young Bowfin can be quite active in swimming and in pursuit of live food. Within a few months they usually become too large for most aquarium keepers and are less active during the day.

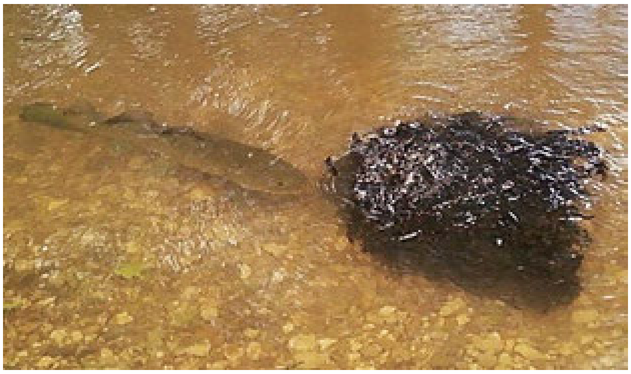

Figure 8.12. A male Bowfin, *Amia calva*, with his pod or swarm of young (the large black ball). Photograph from southern Indiana, taken on 5 May 2011 (used with permission of Bowfin Anglers Group 2011, www.bowfinanglers.com).

REPRODUCTION

One aspect of Bowfin natural history that is generally ignored in the phylogenetics of so-called ancient fishes is the fact that *Amia calva* builds a nest and only the male guards its young. This highly specialized reproductive mode is unlike any of the living ancient fish lineages in North America (e.g., Sturgeons, Paddlefishes, Gars), which are made up of broadcast spawners that do not build nests or show parental care-giving behaviors. Only in Ictaluridae (North American Catfishes) and Centrarchidae (Sunfishes), lineages distantly related to Bowfins, do we encounter nest building, parental guarding, and care-giving behaviors.

Sexual Maturity

Male Bowfin mature at ages 2–4 (<400–457 mm TL, 15.7–18.0 inches) and females at ages 2–5 (<400–610 mm TL, 15.7–24.0 inches) (Scott & Crossman 1973; Simon 1990; Davis 2006). Mature females from Ohio and Michigan ranged from 483 to 711 mm TL (19–28 inches) and from 2,268 to 3,969 g (5.0–8.8 pounds), but no specific ages were reported (Carlander 1969). Minimum size at maturity is about 380 mm TL (15 inches) (Simon 1990) (Table 8.1).

Sexual Dimorphism

Mature male Bowfin have a distinctive color pattern consisting of a black spot ringed with orange or yellow on the upper caudal rays. Females lack this spot, likely due to inhibition from an ovarian hormone, but young individuals have the spot (Zahl & Davis 1932; Breder & Rosen 1966; Becker 1983). Breeding males have turquoise blue-green coloring on the lips, throat, belly, and ventral fins (Page & Burr 2011) (Fig. 8.13). Females are usually darker and duller than males, always with brownish-red fins (Reighard 1903). Females also tend to be larger than males (Carlander 1969; Becker 1983; Koch et al. 2009b).

Table 8.1. Summary of life history characteristics of Amiidae based on the Bowfin, *Amia calva*, the only extant member of the family.

Number of species	1 extant; about 30 extinct
Salinity	Primarily freshwater but also brackish; 1.6–18 ppt
Maximum size	109 cm (42.9 inches) TL; 9.75 kg (21.5 pounds)
Maximum age	13 years (wild); 30 years (captive)
Age and size at first reproduction	2 years; <400 mm (15.7 inches) TL
Iteroparous or semelparous	Iteroparous
Fecundity estimates (ovarian counts)	9,498–110,086
Mature egg diameter	2.2–3.0 mm (0.08–0.12 inch)
Egg deposition sites	Circular clearing in vegetation to which eggs adhere
Clutch size	2,000–5,000
Range of nesting and spawning dates and temperatures	Late February–June; 16–19°C (60.8–66.2°F)
Habitat of spawning sites; average water depth	Clearing of vegetation with roots, sand, or gravel at depths of 0.5–1 m (1.6–3.3 feet)
Incubation period	6 days at 16–17°C (60.8–62.6°F)
Mean size at hatching	3–7 mm (0.12–0.28 inch) TL
Parental care	Male prepares nest and guards young, often attacking intruders or dispersing young upon being disturbed
Major dietary items	Fish, crayfish, aquatic amphibians, other aquatic macroinvertebrates, and insect larvae
General year-round habitat	Medium to large low-gradient creeks and rivers and associated floodplains and off-channel habitats
Migratory or diadromous	Nonmigratory; may make short-distance movements en masse into flooded habitats for spawning
Imperilment status	Not imperiled range-wide; protected in Pennsylvania as "candidate" species

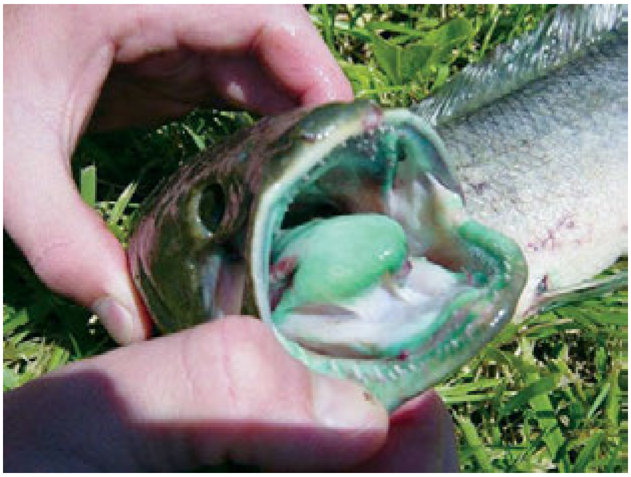

Figure 8.13. Turquoise blue-green lips and mouth of breeding male Bowfin, *Amia calva*. Photographed on 5 May 2009 in southern Illinois (used with permission of Bowfin Anglers Group 2011, www.bowfinanglers.com).

Spawning Migrations

Bowfin move into backwaters, sloughs, floodplain habitats, and tributaries during spring for nest building and spawning (Dean 1898; Eddy & Underhill 1974; Simon 1990). A more detailed examination of pre-spawning movements is lacking.

Seasonality

Bowfin reproduce in spring and early summer when water temperatures reach 16–19°C (60.8–66.2°F). More southern populations begin spawning as early as late February (Louisiana), March, or early April (Louisiana, Tennessee, Missouri, Arkansas) and northern populations end spawning as late as June (Michigan, Ontario) (Doan 1938; Scott & Crossman 1973; Robison & Buchanan 1984; Simon 1990; Etnier & Starnes 1993; Davis 2006) (Table 8.1).

Spawning Mode, Behavior, and Habitat

Bowfin spawn in circular clearings of vegetation (0.5–1 m diameter, 1.6–3.3 feet; 10–20 cm depth, 3.9–7.9 inches; Fig. 8.14) or exposed roots. The male clears the nest area usually at night in shallow to moderately deep water

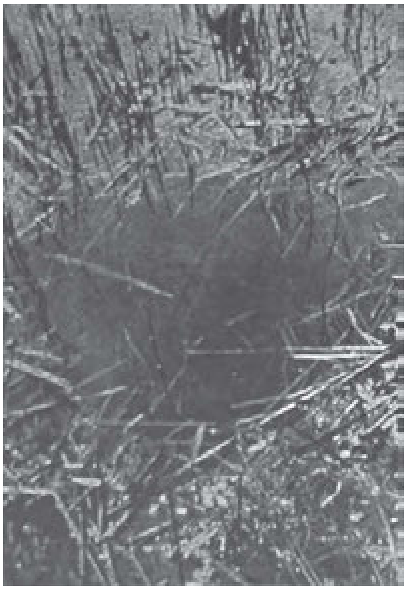

Figure 8.14. Example of the nest of the Bowfin, *Amia calva*, consisting of a circular clearing in a heavily vegetated area (from Dean 1898).

(≥0.5–1.2 m, 1.6–4.0 feet) by removing leaves and stems, probably through biting, leaving a trough 10–20 cm (3.9–7.9 inches) deep with roots, sand, or gravel for the eggs. Spawning also occurs under logs, stumps, and bank vegetation and over mud substrates (Breder & Rosen 1966; Green 1966; Robison & Buchanan 1984; Simon 1990). Nesting is usually in colonies (Carlander 1969; Robison & Buchanan 1984). Nests can be close together with one observer noting 11 nests within a 15 m (49 feet) radius (7 within a 4.5 m radius, 14.8 feet; Dean 1898), though this is contradicted by other observers who found nests much farther apart (Whitman & Eycleshymer 1897). After constructing a nest, a male waits for females to arrive, and courtship, consisting of bouts of caressing, biting, and circling followed by side-by-side positioning, agitated fin movement, and milt/egg release, commences. Before spawning, the male Bowfin takes the female's snout (both upper and lower jaws) into his mouth while the female remains motionless, only moving her fins. After this, the male often circles the female in various positions for 15–20 min before eggs are laid (Reighard 1903). These courtship sessions, usually also occurring at night, can last ≤1.5 h and may occur ≤6 times, although the spawning event itself lasts ≤1 min (Reighard 1903; Breder & Rosen 1966; Becker 1983). Males may battle for spawning rights with a female (Whitman & Eycleshymer 1897). Males and females can both mate with multiple individuals during a season (Reighard 1903; Breder & Rosen 1966; Scott & Crossman 1973), and are suspected of even spawning in groups of a female and several males (similar to Lepisosteidae), although this is supported by only a single observation of multiple males at a nest after spawning had commenced (Dean 1898).

Parental Care

Male Bowfin guard fertilized eggs and juveniles until these reach about 100 mm TL (3.9 inches) (Breder & Rosen 1966) with juveniles forming schools sometimes of ≥5,500 individuals (Fig. 8.12) (Boschung & Mayden 2004). Guarding males often attack any object thrust into the water appearing to threaten the young, violently rushing and striking it, even to the point of coming out of the water, then retreating some distance (about 2 m, 6.6 feet), and turning swiftly to make another attack (Kelly 1924; Breder & Rosen 1966). Another report suggests a less aggressive response in which a male swiftly darted away from an intruder, dispersing the school of young and stirring up the substrate, roiling the water, and providing cover to the young. The male then returned, unseen, after 5 min by navigating under the substrate debris, and the young re-formed in a school near the male (Doan 1938). During either of these responses by the male, juveniles disperse and retreat to vegetative cover, although Dean (1898) reported that schools of young remained undispersed despite his many advances on the male and young. Male Bowfin also keep conspecifics away from the guarded nest (Reighard 1903). This guarding behavior is interrupted at times by periods of absence from the nest area, noted more frequently in the morning (Reighard 1903). If a protecting male dies or does not return to his young, the swarm is in danger of predation and may unite with the swarm of another male (Reighard 1903).

Reproductive Allocation

Reports of fecundity vary, likely due to differences in methods used, though these were not always reported. Studies likely using ovarian oocyte counts from body cavities of mature fish (483–843 mm TL, 19.0–33.2 inches) found between 9,498 and 110,086 oocytes (MacKay 1963; Carlander 1969; Eddy & Underhill 1974; Simon 1990; Davis 2006); however, most studies document fecundity values of <80,000 (but see Simon 1990 and outliers in Koch et al. 2009b). Other studies observed nests containing between 2,000 and 5000 eggs

(Breder & Rosen 1966; Simon 1990). Gonad somatic index (GSI, weight of gonads / total weight of fish × 100) values for mature female Bowfin in two pools in the Mississippi River ranged from 1.9% to 14.8% (mean 9.5%) (Koch et al. 2009b). More detailed studies of oocyte maturation stages (sensu Heins & Baker 1993; Baker & Heins 1994) and nest clutch sizes are needed. Eggs are 2.2–3.0 mm (0.09–0.12 inch) in diameter (Simon 1990) (Table 8.1).

Egg, Embryo, and Larval Development

Eggs are elliptical and adhesive, sticking to exposed roots and plants in and near the nest. They range in color from cream yellow when laid to much darker with age but also vary geographically (Breder & Rosen 1966; Simon 1990). Seven cleavage stages begin at about the following times after oviposition: first, 2.24 h; second, 3.28 h; third, 4.20 h; fourth, 5.20 h; fifth, 6.20 h; sixth, 7.25 h; late cleavage, 10 h. Blastula and early gastrula stages begin at 15-h and 40-h post-oviposition, respectively. Embryos become visible around 70-h post-oviposition and begin to move at around 160 h (Whitman & Eycleshymer 1897). Eggs incubate for 4–14 days depending on temperature (6 days at 16–17°C, 60.8–62.6°F) with yolk-sac larvae hatching at 3–7 mm TL (0.12–0.28 inch) (Becker 1983; Simon 1990). Early yolk-sac larvae (4.4–6.9 mm TL, 0.17–0.27 inch) appear tadpole-like with a nonfunctional eye bud and prominent adhesive organ that is used to attach to structures and maintain position. The mandible begins forming at 6 mm TL (0.24 inch), and pectoral fin formation begins. In older yolk-sac larvae (7–9 mm TL, 0.28–0.35 inch) the head region enlarges, the yolk sac reduces in size, the operculum begins developing, the auditory vesicles become evident, and first dorsal and anal rays are formed. By 9–10 mm TL (0.35–0.39 inch), the adhesive disc is absorbed or greatly diminished, the mandible is clearly visible, the lateral line is developed, the gular plate is formed, and fin-ray formation continues with pelvic fins first appearing at 10–11 mm TL (0.39–0.43 inch). The yolk sac is usually absorbed by 10 mm TL (0.39 inch) but may remain until 13.2 mm TL (0.52 inch). In post-yolk-sac larvae (11–30 mm TL, 0.43–1.18 inch), nasal openings form, formation of the lateral line extends to the anal fin, fin differentiation and formation are completed, and scales become visible (26 mm TL, 1.02 inches) (Simon 1990) (Figs. 8.15–8.17; see detailed account of ontological changes by Jaroszewska & Dabrowski 2009) (Table 8.1).

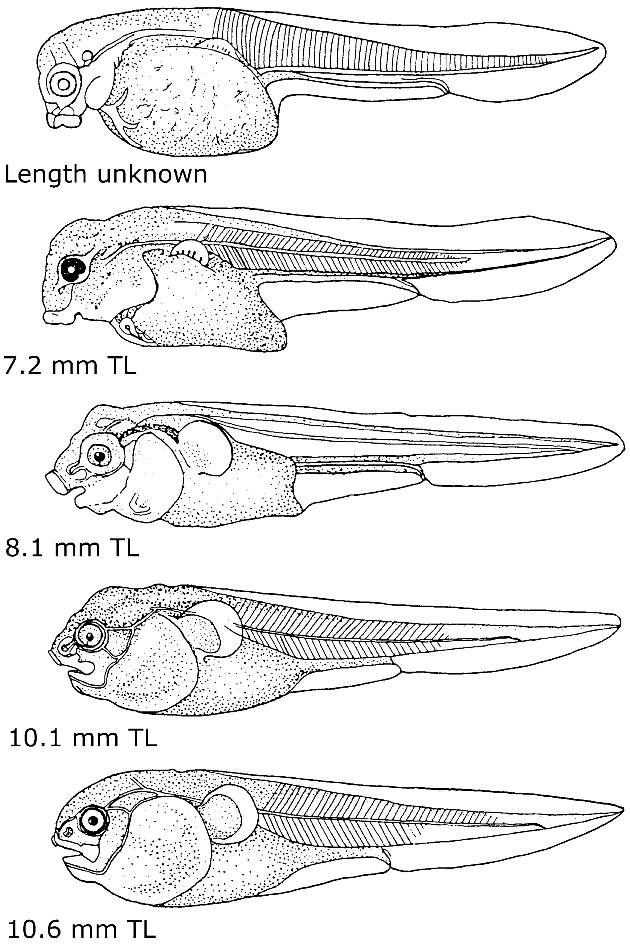

Figure 8.15. Development of young Bowfin, *Amia calva*. Yolk-sac larvae (modified from Jones et al. 1978, federal government publication in the public domain).

Gametes

Bowfin sperm exhibit several notable features, including mitochondrial matrix granules that are thought to be binding sites for calcium (Young et al. 2006) and pores open to the cell surface that are unusual for fish spermatozoa (Jamieson 1991; Mattei 1991; Quaggio-Grassiotto et al. 2001). Like Gars and other neopterygian fishes, Bowfin sperm lack an acrosome, the cap covering the head of the sperm containing chemicals used to penetrate the outer layer of the egg (chorion). In contrast with sperm of Gars, Bowfin sperm have a rounded rather than an oval-shaped head, the centrioles are located some distance from rather than close to the nucleus, and side fins on the flagellum are lacking (Afzelius & Mims 1995). Bowfin eggs are elongate in form and possess a compact membrane with extended projections that help the eggs attach to underwater vegetation (Jaroszewska & Dabrowski 2009).

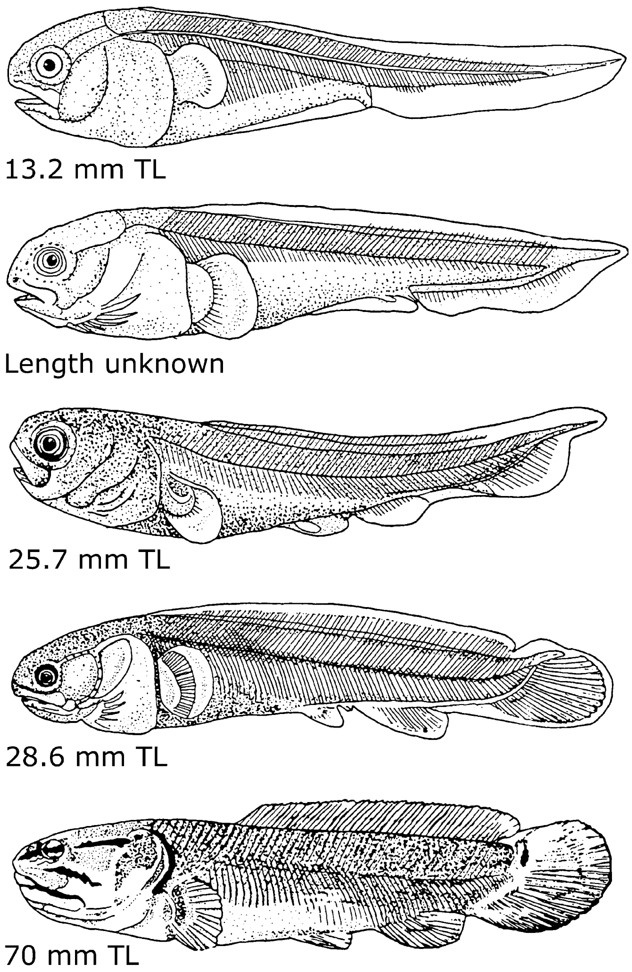

Figure 8.16. Development of young Bowfin, *Amia calva*. Post-yolk-sac larvae (modified from Jones et al. 1978, federal government publication in the public domain).

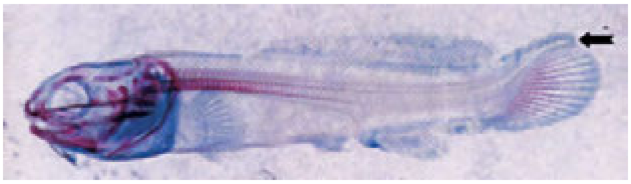

Figure 8.17. Cleared-and-double-stained (cartilage is blue, bone is red) specimen of young Bowfin, *Amia calva* (27 mm TL), in early stages of fin-ray development. Heterocercal tail indicated with arrow (from Grande and Bemis 1998; used with permission of L. Grande).

ECOLOGY

Habitat

Bowfin inhabit medium to large low-gradient creeks and rivers and the side channels, sloughs, oxbows, seasonal floodplains, lakes, wetlands, and artificial ponds connected to or associated with these drainages (Dence 1933; Carlander 1969; Becker 1983; Simon 1990; Baker et al. 1991; Heatherly et al. 2005; Smith et al. 2006; Driver et al. 2009). Within this larger habitat template, Bowfin occur in a number of microhabitats, including pools (Smith et al. 2006, no depth given) and shallow water depths (Dence 1933), often in waters with a variety of abundant vegetation (Carlander 1969; Becker 1983; Driver et al. 2009), but usually in pools or backwaters. Bowfin occasionally occur in brackish estuaries and coastal marshes where salinity can be relatively high (e.g., Gunpowder River estuary, Chesapeake Bay, Maryland, Pearson & Ward 1972; Intercoastal Waterway, Calcasieu River, Louisiana, Stacy et al. 1970) (see physiology section). The Bowfin is often classified as a pollution-tolerant species (Trexler 1995; Tabit & Johnson 2002; Webb 2008) and can be found in highly modified artificial or urban-impacted habitats (Dence 1933; Chipman 1959; Farabee 1986; Trexler 1995; Tabit & Johnson 2002; Webb 2008; Driver et al. 2009). Young-of-the-year and juvenile Bowfin (≤60 mm TL, 2.36 inches) occupy shallow water (≥150 mm, 5.9 inches) in vegetation at least until no longer guarded by the male (about 100 mm TL, 3.9 inches), but young-of-the-year may occur in main channel border, tributary, and side channel habitats in the upper Mississippi River (Barko et al. 2004). The small number of juveniles captured after this stage suggests that older juveniles move to deeper or more densely vegetated habitats (Simon 1990).

Diet

Adult Bowfin are apex predators (one of only two native piscivores in most east coastal drainages; MacAvoy et al. 2000), feeding predominantly on aquatic vertebrates, including most families of fishes, amphibians (frogs, amphiumas, sirens, newts) and reptiles (snakes), and invertebrates, mainly crayfishes. They use both their forward movement and suction to capture prey. The opening and closing of the mouth during prey capture takes only 0.075 s. They differ from most other fishes in their extreme depression of the floor of the mouth (area of gular plate and branchiostegal rays) after the mouth is closed during feeding (Lauder 1979). Other invertebrates including crabs, shrimps, mollusks, snails, amphipods, isopods, and dragonfly (Anisoptera) and damselfly naiads as well as aquatic beetle (Dytiscidae), blackfly (Diptera), mayfly (Ephemeroptera), and caddisfly (Trichoptera) larvae, water striders (Gerridae), Hemiptera, earthworms, and leeches are also consumed but usually make up a small percentage of diet by number and volume or are only occasionally eaten (Nurnberger 1930; Lagler & Hubbs 1940; Lagler & Applegate 1942; Stacy et al. 1970; Dugas et al. 1976; Jordan & Arrington 2001). Plant material is consumed as well, perhaps incidentally when engulfing prey items (Stacy et al. 1970; Dugas et al. 1976). Adult Bowfin also consume aquatic birds (Gowanloch 1933; Stacy et al. 1970) and are cannibalistic (Lagler & Applegate 1942; Simon 1990) (Table 8.1). A large proportion of empty stomachs was noted in several studies (45%, Lagler & Applegate 1942; 70%, Dugas et al. 1976; 19%, Arrington et al. 2002; 100%, Nurnberger 1930) and was sometimes thought to be associated with traps (Lagler & Applegate 1942) but capture method was not always reported (Nurnberger 1930). In the Atchafalaya Basin, Louisiana, during low-water periods adult Bowfin tended to consume more fishes and shrimp, but more crayfishes were eaten during high-water periods, similar to the dietary habits of other predatory fishes (Dugas et al. 1976). The species apparently does not scavenge or feed on carrion (Reighard 1903). Bowfin exhibit substantial differences in individual feeding behavior and history as revealed by stable isotope analyses (Fry et al. 1999).

Although the large list of prey items above documents the opportunistic nature of Bowfin feeding, studies of captive feeding trials documented preferences for Fathead Minnows (*Pimephales promelas*) and Virile Crayfish (*Orconectes virilis*) over Sunfishes (mostly Bluegill, *Lepomis macrochirus*, but also Green Sunfish, *Lepomis cyanellus*, and Pumpkinseed, *Lepomis gibbosus*) (Mundahl et al. 1998). Nevertheless, another captive study found preference for *L. cyanellus* over *L. macrochirus* over Golden Shiners, *Notemigonus crysoleucas*, over Largemouth Bass, *Micropterus salmoides* (Herting & Witt 1967). Adult Bowfin generally display no size selectivity with fishes to the limit of their gape capacity (Mundahl et al. 1998), but prey size increases with Bowfin length (Jordan & Arrington 2001). No evidence exists of major differences in diet composition based on size, sex, or season in adult Bowfin (Stacy et al. 1970), except with regard to water level in the Atchafalaya Basin (Dugas et al. 1976), although few diet studies have examined these factors in detail. Feeding activity may be greater at night (Carlander 1969) or may be crepuscular (Reighard 1903).

Juvenile Bowfin (35–70 mm TL, 1.4–2.8 inches) feed mainly on planktonic crustaceans (cladocerans, amphipods, copepods) and adults and naiads of Odonata. Also consumed in smaller numbers are Chironomidae and other dipteran larvae. Plant material, mostly filamentous algae, is frequently found in juvenile stomachs (Schneberger 1937; Stacy et al. 1970; Simon 1990). Small juveniles (<50 mm TL, 2.0 inches) consume fewer and smaller odonates, amphipods (*Hyalella*), and chironomids (Schneberger 1937). In an aquarium setting, 10 young Bowfin (44–70 mm TL, 1.7–2.8 inches) vigorously attacked and consumed a dozen Largemouth Bass fry (about 19 mm TL, 0.75 inch) in seconds and regularly took beef kidney and liver thereafter (Schneberger 1937). As observed in aquaria, young Bowfin move and feed constantly, pausing only to surface for gulping air. This constant activity decreases with size (Simon 1990). Young-of-the-year Bowfin reared at 26.2°C (79.2°F) consumed an average daily food ration of 6.48% of body weight (Herting & Witt 1968).

Age, Growth, and Mortality

A variety of structures are used in aging Bowfin, including otoliths, vertebrae, scales, branchiostegal rays, gular plates, and pectoral and pelvic fin rays (Holland 1964; Schiavone 1982; Mundahl et al. 1998; Davis 2006; Koch et al. 2009a). Of two comprehensive investigations, one found the lowest variation in age estimation with cross sections of pectoral and pelvic fin rays; gular plate sections also were fairly readable (Koch et al. 2009a). The other found only gular plates useful for age estimates (Holland 1964). Other structures were either unreadable or provided no annuli.

Bowfin are relatively long-lived fish, even in the wild. In studies on the Mississippi River, 257 Bowfin from 392–807 mm TL (15.4–31.8 inches) were 2–13 years old based on estimates from fin ray and gular plate sections (Koch et al. 2009ab). Individuals in captivity have lived for ≥20–30 years (Carlander 1969). In the upper Mississippi River, males have lower longevity (9 years maximum) and higher mortality rates (33–37%) than females (13 years maximum; 24–26%), perhaps due to their territorial nest- and young-guarding behavior (Koch et al. 2009b). Koch et al. (2009b) estimated total annual mortality in the upper Mississippi River at about 35%, but this was much lower than a Louisiana estimate of 58% (Davis 2006). Maximum length is 109 cm TL (43 inches) (Page & Burr 2011), and the maximum recorded weight is the world angling record from South Carolina, 9.75 kg (21.5 pounds) (IGFA 2011).

Early growth of Bowfin is rapid, with individuals averaging >50 mm (2 inches) growth in a month's time from mid-April to mid-May in Missouri. Growth/day averaged

3.7 mm (0.15 inch) for a 3-day period in mid-April, slowed for the rest of the month, and increased again in early May when the diet switched from mostly Cladocera to small fishes and crayfishes (Simon 1990). Some individuals may exceed 203 mm TL (8.0 inches) in their first year of life (Becker 1983).

Population Sizes and Densities

Bowfin range from uncommon to locally common, depending on habitat (Becker 1983; Page & Burr 2011), but few studies have explicitly examined population sizes and densities of Bowfin populations. The limited information that can be inferred from other types of studies indicate low (0.019 individual/ha, 0.008 individual/acre) to moderate (3.17 individuals/ha, 1.28 individuals/acre) densities in a large river pool (Koch et al. 2009b) and vegetated lake habitat (Shireman et al. 1981), respectively. In the past the population in the Suwannee River near the Okefenokee Swamp was described as phenomenal, making up 82% of the total fish biomass (373 of 457 kg, 823 of 1,000 pounds) in rotenone samples from that section of the river (Holder 1970). The density was roughly 242 individuals/ha (98 individuals/acre). Within the swamp, Bowfin constituted only 30% of the fish biomass and occurred at densities of about 9.9 individuals/ha (4 individuals/acre).

Predation

Adult and juvenile Bowfin are susceptible to predation from a number of vertebrates, including the American Alligator, *Alligator mississippiensis* (Giles & Childs 1949; Delany & Abercrombie 1986; Valentine et al. 1972; Rice et al. 2007); Bald Eagle, *Haliaeetus leucocephalus* (McEwan & Hirth 1980); Great Egret, *Ardea alba* (Smith 1997); Great Blue Heron, *Ardea herodias* (Hoffman & Curnow 1979); and Wood Stork *Mycteria americana* (Ogden et al. 1976; Depkin et al. 1992). Nevertheless, Bowfin usually make up a relatively small percentage of predator diet (1.5–11% volume, American Alligator; 0.1–13.3% mass, Wood Stork; 0.5% mass, Great Egret). Bowfin also are consumed as carrion by turtles (Lagler 1943) and the Bald Eagle (Dunstan & Harper 1975). As noted, adult Bowfin also eat juveniles (Lagler & Applegate 1942).

Parasites

Bowfin are parasitized by a number of ecto- and endoparasitic invertebrates including protozoans (2 species), trematodes (19), cestodes (9), nematodes (7), acanthocephalans (9), leeches (1), copepods (2), tongue worms (1), and mites (1) (Leidy 1886; Ward & Magath 1916; Essex 1929; Winfield 1929; Thomas 1930; Hunter 1932; Dolley 1933; Mueller 1936; Meinkoth 1947; Lincicome & VanCleave 1949; Bangham 1955; Stunkard 1956; Ash 1962; Sillman 1962; Font & Corkum 1975; Taylor 1978; Robinson & Jahn 1980; Thomas 1983; Amin 1989; Jones & Woo 1992; Joy 2008; de Chambrier et al. 2009; Joy et al. 2009). Probable vertebrate ectoparasites include the Silver Lamprey, *Ichthyomyzon unicuspis*, and Chestnut Lamprey, *Ichthyomyzon castaneus* (Hubley 1961). Freshwater mussels using Bowfin as hosts (i.e., larval transformation observed) include the Fluted-shell, *Lasmigona costata* (Hove et al. 1994), and Washboard, *Megalonaias nervosa* (Howard 1914b; Becker 1983). Golden Shiners, *Notemigonus crysoleucas*, are social parasites (nest associates) of Bowfin, but the Bowfin may benefit from the interaction by a lower probability of egg consumption in a nest with higher egg density (Katula & Page 1998).

CONSERVATION

Commercial and Recreational Fishery Regulation

In most U.S. states Bowfin are not protected by fishing regulations, and in some states their destruction and take are encouraged by open seasons and fishing methods (e.g., Arkansas, AGFC 2007). Some states have size limits on Bowfin with the goal of preserving long-term yields (e.g., 40.6 cm TL, 16 inches, recreational; 55.9 cm TL, 22 inches, commercial in Louisiana, LDWF 2011ab) or have regulations on roe harvesting (LDWF 2011b). Pennsylvania lists the Bowfin as a candidate species (a species that could be recognized as Threatened or Endangered in the future) and encourages immediate release if caught (Commonwealth of Pennsylvania 2011). Suggested minimum harvesting size to prevent recruitment overfishing was 63.5 cm TL (25 inches) in the upper Mississippi River (Koch et al. 2009b), substantially greater than the minimum sizes established in Louisiana.

COMMERCIAL IMPORTANCE

Subsistence, Recreational, and Commercial Uses

Although not generally considered of great economic importance, native cultures of North America used Bowfin

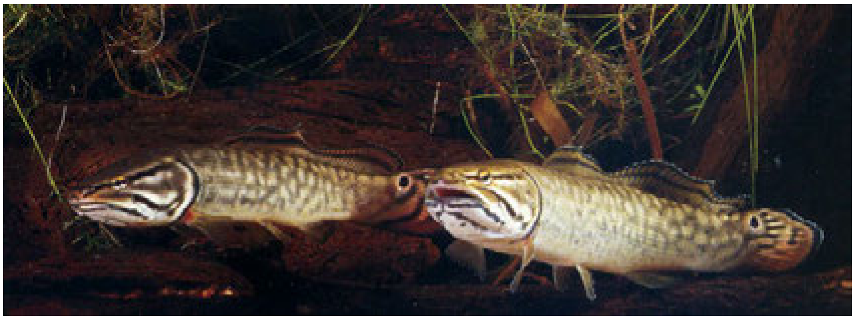

Figure 8.18. Two Bowfin, *Amia calva* (photograph by and used with permission of D. E. Scott).

widely. Bowfin remains, although mostly found in small numbers, were unearthed in archaeological digs at settlement sites inhabited between about 5,000 BP and 1814 throughout the Southeast (Alabama: Jackson & Scott 2003; Pavao-Zuckerman 2007; Georgia: Keene 2004) and Midwest (Illinois: Munson et al. 1971; Parmalee 1962; Indiana: Stafford et al. 2000; Michigan: Lovis 1985).

In modern times, Bowfin are sometimes kept as pets in aquaria (e.g., Wolff 1996; Scharpf 2013). They are normally not sought out as a food fish but are taken and consumed opportunistically, more so by African Americans (Burger et al. 1999, 2001ab). Many sources indicated they are unpalatable or distasteful (Reighard 1903; Becker 1983; Jenkins and Burkhead 1994); however, others considered the taste of their meat quite good (Burr & Warren 1995). In southeastern Missouri, Bowfin made up about 4.5% of total sportfish caught (Pflieger 1997). Despite this, significant commercial takes occur from the Mississippi River using trot lines, gillnets, and other types of nets with hauls from Wisconsin waters averaging >2,900 kg (6,393 pounds) of fish/year from 1956 to 1975. The largest single take during this period was 5,626 kg (12,403 pounds) in 1961. In 1975, Bowfin brought Wisconsin commercial fishers \$0.04/kg (\$0.02/pound, Becker 1983). Bowfin roe is also marketed as specialty caviar, and prices in Tennessee increased from \$15/kg (\$6.81/pound) in 2005 to \$80/kg (\$36.40/pound) in 2008 (Koch et al. 2009b). Prices from a search of about 15 online retailers (March 2009) of the eggs revealed even higher prices, ranging from \$0.28 to \$0.74/g (\$8–\$21/ounce). Studies of Bowfin have revealed high levels of mercury (study averages ranged from 0.45 to 0.94 ppm) and other heavy metal contamination (e.g., strontium, cesium) compared with other fishes, thus potentially increasing risk of poisoning or cancer if consumed (Cumbie 1975; Francis et al. 1998; Burger et al. 2001ab; Glover et al. 2010).

Use in Fisheries Management

Although the Bowfin, along with Gars, have often been considered a nuisance species worthy of wholesale eradication for their perceived voracious consumption of valuable gamefishes (e.g., Dean 1898; quotes and accounts in Scarnecchia 1992), more level-headed, holistic fisheries researchers have emphasized the ecological role of Bowfin in freshwater food webs (Ricker 1946; Scarnecchia 1992). Because Bowfin often eat smaller individuals of popular sportfishes (e.g., consume Bluegill <92 mm TL, 3.6 inches, Dugas et al. 1976; or averaging 73 mm TL, 2.9 inches, Mundahl et al. 1998), their importance to sport fisheries could be significant if they consume enough juveniles to prevent overpopulation and stunted growth (Ricker 1946; Scarnecchia 1992). On the other hand, as many diet studies reveal, Bowfin predation on sportfishes is usually limited (Herting & Witt 1967; Mundahl et al. 1998), and their usefulness as population regulators can be further limited by other factors such as lack of reproductive success in some conditions (Mundahl et al. 1998). Regardless of their utility for population control, Bowfin (Fig. 8.18) add important diversity, in terms of both evolutionary history and ecological function, to the communities in which they live, a fact hopefully being increasingly recognized by fisheries professionals (Scarnecchia 1992).

LITERATURE GUIDE

Several edited volumes and books offer good overviews of Bowfin biology. Jaroszewska & Dabrowski (2009) provided an important review of early development in Bowfin and Gars. Simon (1990) summarized many difficult-to-find sources, especially on early life history and development. Grande & Bemis (1998), in a nearly 700-page monograph, reviewed and analyzed the morphology of the living Bowfin and all of its fossil relatives. The monograph is profusely illustrated and is simply indispensable for anyone doing comparative studies on amiids and their relatives. Reighard (1903) studied the natural history of Bowfin in the Huron River system near Ann Arbor, Michigan, from 1891 to about 1902. He reviewed all the historical literature to that point and conducted careful observations of embryos, nests, adults, the swarms of young, and other aspects of the life history. Most of what we know about the everyday life of the species is the result of Reighard's meticulous studies.

Acknowledgments

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Chapter 9 Hiodontidae: Mooneyes

Eric J. Hilton, William E. Bemis, and Lance Grande

The family Hiodontidae, the Mooneyes (subdivision Osteoglossomorpha, order Hiodontiformes), contains two species that are considered living fossils and are similar to other basal groups of fishes (e.g., Gars, Lepisosteidae; Bowfins, Amiidae) in having a long fossil record from the fresh waters of North America and being species-poor relative to the extant fauna. The sister-order to the Mooneyes, the Osteoglossiformes (Bonytongues), are also freshwater and found in South America, Africa, Southeast Asia, and northern Australia (the fossil record of the osteoglossomorphs includes several marine taxa, and the group is found on all continents except Antarctica). In contrast to Hiodontiformes, the Osteoglossiformes are quite diverse (4 families, 28 genera, 218 species) and include one of the world's largest freshwater fishes (to 2.5 m TL), the Pirarucú (*Arapaima gigas*) of South America. Most of the diversity of the Osteoglossiformes is found in a single family, the Elephantfishes of Africa (Mormyridae; 18 genera and >200 species), which can transmit and detect weak electric currents, have a large brain comparable in relative size to the human brain, and appear to have considerable learning capability (e.g., Cain & Malwal 2002; Nelson 2006; Walton & Moller 2010).

Mooneyes superficially resemble shad of the family Clupeidae, the Herrings, but can be distinguished by the absence of abdominal scutes and the presence of strongly developed dentition on the basibranchial and basihyal toothplates. The name *Hiodon* means "toothed hyoid" and refers to particularly well-developed teeth on the basihyal toothplate. This gross morphological similarity to Herrings is reflected in the species epithet for the Goldeye (*alosoides*), which denotes similarity to the shad genus *Alosa*. Mooneyes are generally silvery fish, and the specific epithet for the Mooneye (*tergisus*) means "polished."

DIVERSITY AND DISTRIBUTION

Extant Mooneyes occur only in North America and are represented by one genus with two species: *Hiodon tergisus*, the Mooneye, and *H. alosoides*, the Goldeye (Table 9.1). The two species have broadly overlapping ranges throughout much of the central and eastern parts of North America (Fig. 9.1). Their ranges are remarkably broad latitudinally, extending from the southernmost portion of the Mississippi River drainage to the far northwestern drainages of the Northwest Territories. The range of the Goldeye extends farther north than that of Mooneye, following the Mackenzie River to its entrance into the Beaufort Sea. An isolated population of Goldeyes also occurs in the southern tributaries of James Bay, Quebec and Ontario. Species of *Hiodon* were present west of the North American Continental Divide until the Miocene (25–5 mya; G. R. Smith 1981; Cavender 1986). In contrast to many other widely distributed fishes, phylogeographic variation is unstudied within the Goldeye and Mooneye.

Non-Native Distribution

Both species of the genus have been introduced outside of their native ranges but only to a limited extent. In Nebraska, the Goldeye was stocked in the White River in 1896 and Lake Minatare in 1952; Mooneyes were introduced in a canal in Washington County, Maryland, in the late 1800s. All these stockings apparently were unsuccessful, and the

Table 9.1. Life history traits of *Hiodon*. Data from Battle & Sprules (1960), Kennedy & Sprules (1967), Scott & Crossman (1973), Donald & Kooyman (1977ab), and Wallus (1990b); also see references in text.

Life History Attribute	**Description**
Number of extant species	Two
Strictly freshwater (ppt)	Yes (precise thresholds unknown)
Maximum size recorded in length and weight	445 mm TL; 1.1 kg
Maximum age	Most estimates 14 years, but possibly to 30 years[1]
Age and size at first reproduction	3–5 years, possibly younger or older depending on latitude; females typically 1 year later than males; 228–280 mm TL
Iteroparous or semelparous	Iteroparous
Fecundity estimates (ovarian counts)	3,000–25,000; average about 13,000, but most often less
Mature egg diameter	About 2.0 mm
Egg deposition sites	Broadcast in current of streams; semi-buoyant eggs drift with current
Clutch size	No nest
Range of spawning dates and temperatures	April–July (peak in April and May throughout most of range); 8–15°C
Habitat of spawning sites; average water depth	Midwater column over rock and gravel, in shallows, usually <60 cm
Incubation period; larval type at hatching	About 2 weeks; proto-larvae
Mean size at hatching	About 7.0 mm TL
Parental care	No known parental care
Major dietary items	Invertebrates, fishes
General year-round habitat	Large rivers, and associated streams, lakes, swamps, and ponds
Migratory or diadromous	Seasonally migratory
Imperilment status	Range margins are being reduced[2]

[1] Donald & Aitken (2005).
[2] NatureServe (2009).

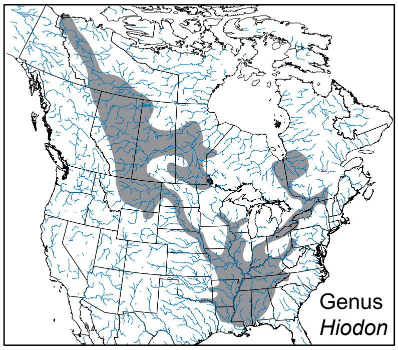

Figure 9.1. Geographic range of the Mooneyes, Hiodontidae.

impacts of their attempted introductions are unknown (Fuller et al. 1999).

PHYLOGENETIC RELATIONSHIPS

Phylogenetic relationships of living and fossil species within *Hiodon* (including species previously classified in the genus †*Eohiodon*) are unclear and need further study (Hilton & Grande 2008). Hiodontidae is part of the group Osteoglossomorpha, the bony-tongue fishes, which is considered by many as the most basal group of teleosts with living representatives (e.g., Patterson & Rosen 1977; but see Arratia 1997, 1999, 2004, in which Elopomorpha—Ladyfishes, Elopidae; Tarpons, Megalopidae; Bonefishes, Albuliformes; Eels, Anguilliformes, and their relatives—takes this position). Two monotypic genera (†*Pleisolycoptera* and †*Yanbiania*) included in the family Hiodontidae (Fig. 9.2) are known from Late Cretaceous deposits of China (89–65 mya; Li & Wilson 1999). Several other putative members of Hiodontidae described from Asia and Eastern Europe are in need of re-examination to verify their taxonomic placement.

Within Osteoglossomorpha, Hiodontidae was once considered the sister-group to Notopteridae + Mormyridae, the Featherfin or Old World Knifefishes and Elephantfishes, respectively (e.g., G. J. Nelson 1968, 1969b; Lauder & Liem 1983). Now, morphological and molecular character data firmly establish that Hiodontidae is the living sister-group to the group containing all other living osteoglossomorphs (e.g., Taverne 1979; Li & Wilson 1996, 1999; Hilton 2003; Lavoué & Sullivan 2004; Zhang 2006; Wilson & Murray 2008). Within Osteoglossomorpha, Hiodon-

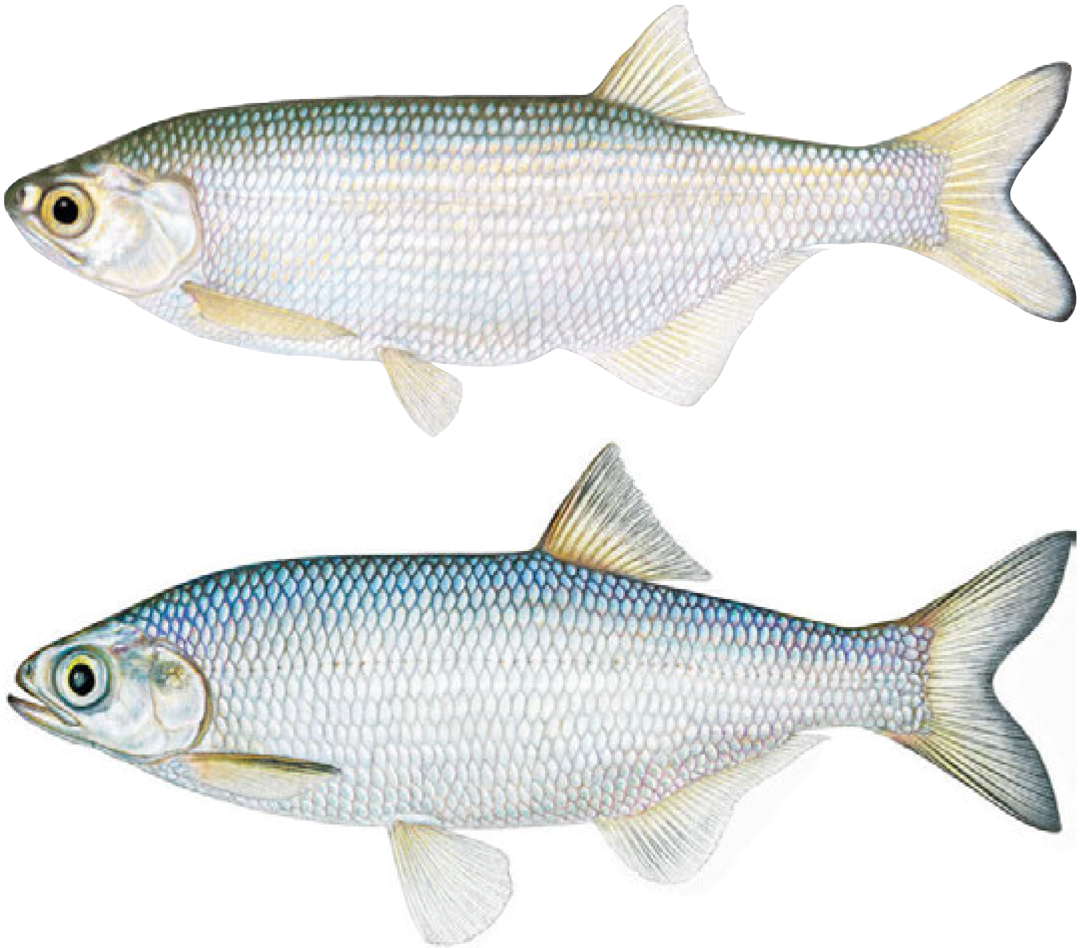

Plate 9.1. (A) Goldeye, *Hiodon alosoides*; (B) Mooneye, *Hiodon tergisus*

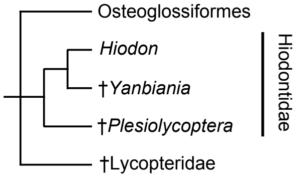

Figure 9.2. Phylogeny of Hiodontidae, the Mooneyes. Hypothesis of relationships among genera within Hiodontidae based on Li & Wilson (1999). Polytomy between Hiodontidae, †Lycopteridae, and all other osteoglossomorph fishes based on Hilton (2003); note evidence exists that puts †Lycopteridae as basal among Osteoglossomorpha generally (Li & Wilson 1999; Zhang 2006; Wilson & Murray 2008) or as sister-group to Hiodontidae (Hilton 2003).

tidae may be sister to †Lycopteridae, a family from the Early Cretaceous (145.5–99.6 mya) of China (Greenwood 1970). Using morphological data, Li & Wilson (1996, 1999), however, resolved †Lycopteridae as basal to all other osteoglossomorphs, including Hiodontidae. Hilton's (2003) subsequent morphological analysis could not resolve this issue, yielding a polytomy among †Lycopteridae, Hiodontidae, and a group containing all other osteoglossomorphs (Fig. 9.2). In an analysis that included more fossil taxa from China (Wilson & Murray 2008), †Lycopteridae was the basal most osteoglossomorph taxon with several other extinct genera (e.g., †*Paralycoptera*, †*Tanolepis*, †*Xixiaichthys*) between †Lycopteridae and the family Hiodontidae.

FOSSIL RECORD

The genus *Hiodon* is known from the fossil record of North America from as early as the Paleocene (65–53 mya; Wilson 1980), although isolated centra identified as belonging to the family Hiodontidae were recovered from the Late Cretaceous Dinosaur Park Formation in Alberta (about 75 mya; Newbrey et al. 2007). Three taxa from the Eocene (55.8–33.9 mya) of North America described in

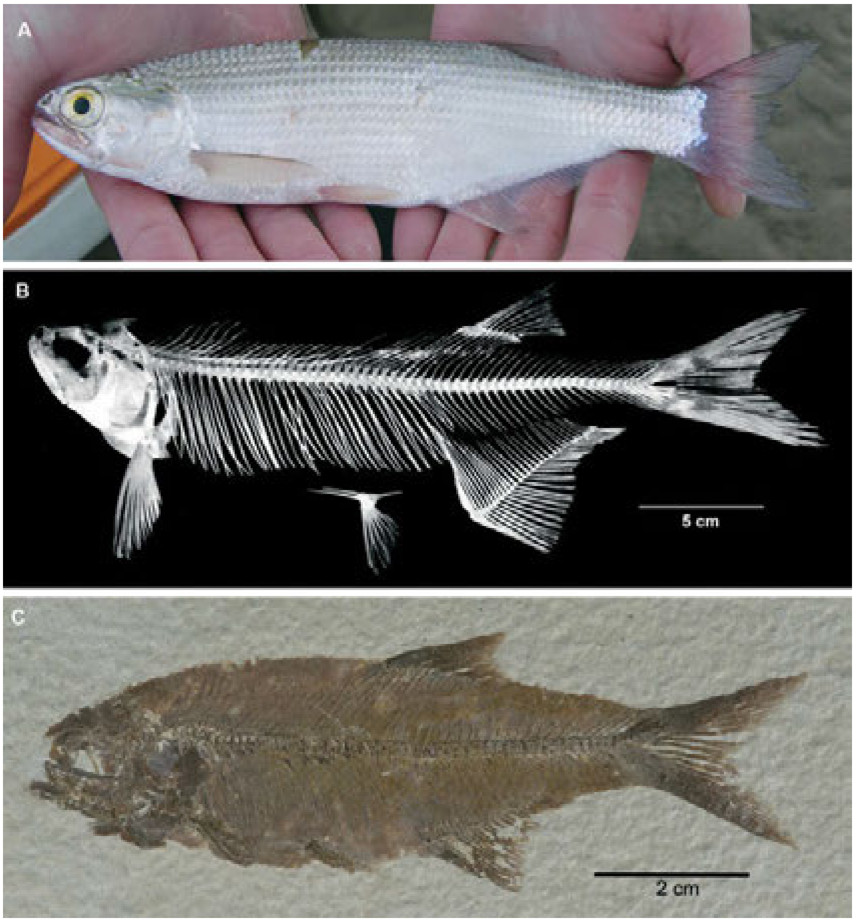

Figure 9.3. (A) Fresh specimen of Goldeye, *Hiodon alosoides*, from the Missouri River. (B) Skeleton of Goldeye, from Lake Sakakawea, North Dakota. (C) †*Hiodon falcatus*, from the Fossil Butte Member of the Green River Formation (52 mya), southwestern Wyoming. Note the differences in the relative position of the anal fin to the dorsal fin in A and B versus C (photographs from Hilton 2002, used with permission of the Field Museum of Natural History).

the genus †*Eohiodon* (Fig. 9.3C; Cavender 1966; Wilson 1978; Grande 1979) were placed subsequently in *Hiodon* (Hilton & Grande 2008). These taxa include †*Hiodon rosei* from British Columbia, †*Hiodon woodruffi* from Washington, Montana, and British Columbia, and †*Hiodon falcatus* from Wyoming, and differ from the extant species by typically having smaller body sizes and lower fin-ray and vertebral counts. †*Hiodon consteniorum* is based on two specimens from the Late Eocene Coal Creek member of the Kishenehn Formation (33 mya) of Montana (Li & Wilson 1994). †*Hiodon lirellus*, considered a nomen dubium (Hilton 2002), was described from fragmentary lower jaw elements from Pleistocene (Blancan Age, 4.5–1.2 mya) deposits of Nebraska (Bennett 1979).

The family Hiodontidae contains at least two other genera that are known exclusively from the fossil record (Fig. 9.2). Both of these genera, †*Yanbiania* and †*Plesiolycoptera*, are monotypic and are from localities in northeastern China (†*Y. wangqingica* from the Early Cretaceous Dalazi Formation and †*P. daqingensis* from the Late Cretaceous Yaojia Formation). Both taxa share with *Hiodon* the presence of seven pelvic fin rays as well as similarly shaped opercles and post-temporal bones. †*Yanbiania* is interpreted to be the sister-group of *Hiodon* because it also has a hyomandibula with two neurocranial articulation heads that are bridged by a thin strut of bone, as is found in the extant genus (Li & Wilson 1999). Fossil otoliths are unknown for the Hiodontidae (Nolf 1985).

MORPHOLOGY

The two species of *Hiodon* are broadly similar in their overall body plan. Both species have a generalized, laterally compressed body, a strongly forked caudal fin, posteriorly positioned dorsal and anal fins, pelvic fins at about mid-body length, and pectoral fins positioned low on the body (Fig. 9.3A). The dorsal and anal fins are slightly falcate, except in mature males, which have rounded anal fins. They are generally silvery in color (slightly blue, to blue-green on the dorsum), and have cycloid scales and a complete lateral-line sensory canal. The mouth is terminal, and the maxillae, premaxillae, and dentary are strongly toothed, as is the basihyal (the tongue) and the parasphenoid. The jaw teeth are relatively larger and fewer in number in the Goldeye than in the Mooneye (Hilton 2002). They lack scales on their head and have a well developed adipose eyelid. The swim bladder is tightly attached anteriorly to the skull. A single, short, and broad pyloric caecum is present in both species of *Hiodon*, and like other bony-tongue fishes, the anterior portion of the intestine passes to the left of the stomach and esophagus (Nelson 1972). This is in contrast to most other Ray-finned Fishes (Actinopterygii) in which the intestine passes to the right of the stomach and esophagus. All other living bony-tongue fishes, except the African Butterfly Fish (*Pantodon buchholzi*), have two moderately long to elongate, digitiform pyloric caeca (Nelson 1972).

Separation of Species

The Goldeye and Mooneye are easily separated based on meristic data (e.g., 9–10 versus 13–16 branched dorsal-fin rays, 30–31 versus 24–27 branched anal-fin rays, 57–62 versus 52–57 lateral-line scales, and 56–61 versus 53–57 preural vertebrae, respectively), position of median fins (dorsal fin insertion anterior of anal fin insertion in the Mooneye, versus above or posterior in the Goldeye), and other morphometric characters (Hilton 2002). The basihyal toothplate is proportionally longer in the Mooneye than in the Goldeye (>65 and 55–60% lower jaw length, respectively). Intraspecific variation exists in both species, including morphometric (Scott & Crossman 1973) and osteological aspects of anatomy of both species. For example, the structure of the caudal skeleton shows individual variation in the Goldeye (Hilton 2002; e.g., the presence of a full neural spine on preural centrum 1 occurred in only about 10% of specimens from Lake Sakakawea, North Dakota).

Skeletal Features

Skeletal anatomy of *Hiodon* is well known (Taverne 1977; Schultze & Arratia 1988; Hilton 2002). In general, the postcranial skeleton of *Hiodon* is relatively primitive (e.g., a single series of intermuscular bones, seven hypurals). The skull, however, is distinctive among teleosts and is dominated by the enlarged, caniniform dentition found along much of the length of the parasphenoid. This dentition is opposed by the similarly enlarged dentition of the basihyal toothplate and is a key component of the so-called parasphenoid tongue bite apparatus (Fig. 9.4). This character was considered a synapomorphy (shared, derived character) of Osteoglossomorpha but is better regarded as a complex of several musculoskeletal features that have evolved in different and novel ways in various groups within osteoglossomorphs as well as independently in other teleostean fishes (Hilton 2001). In addition to the urohyal, the sternohyoideus inserts onto the ventral branchial arches through a tendon that attaches onto the second hypobranchial in *Hiodon* (Greenwood 1971, 1973; Winterbottom 1974; Hilton 2001). Other bony-tongue fishes have a bony process on the second hypobranchial to which the sternohyoideus attaches. This second, more posterior attachment of the sternohyoideus is a unique aspect of the bony-tongue parasphenoid tongue bite apparatus relative to that of other teleostean fishes with a bite between the parasphenoid and hyoid and branchial arches (Hilton 2001).

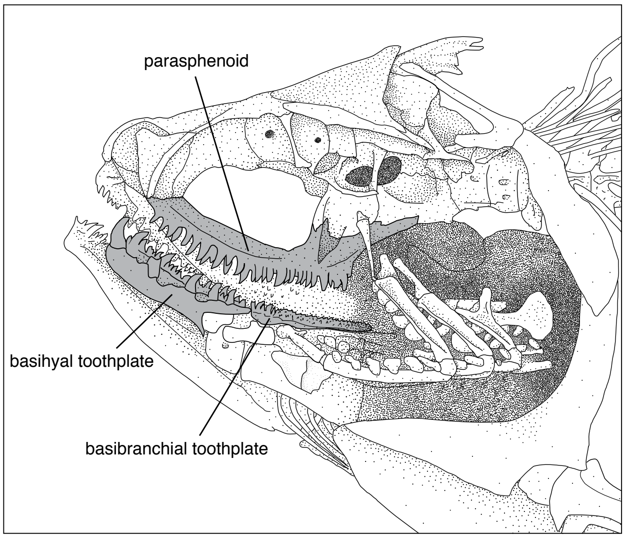

Figure 9.4. The skull and pectoral girdle of an adult specimen of the Goldeye, *Hiodon alosoides*, in lateral view (anterior facing left), showing the so-called parasphenoid tongue bite apparatus. In this specimen the suspensorium and jaws of the left side were dissected away to expose the gill arch skeleton in situ. The toothplates associated with the ventral hyoid and branchial arches occlude with the strongly developed parasphenoid dentition (highlighted in gray) (figure modified from Hilton 2002, used with permission of the Field Museum of Natural History).

Swim Bladder–Ear Connection

The genus *Hiodon* has an otophysic connection between the swim bladder and the inner ear (Greenwood 1973;

Hilton 2002). Although not as well developed or as complex as that of the ostariophysan fishes (Carps, Cypriniformes; Catfishes, Siluriformes; American Knifefishes, Gymnotiformes; and their allies), the swim bladder-ear connection of *Hiodon*, although not studied experimentally, is regarded as a fully functional sound-enhancing mechanism. A pair of cranial diverticula of the anterior end of the swim bladder attach to the basioccipital, exoccipital, and prootic bones of the neurocranium by a thickened peritoneal covering. These three bones define an auditory fenestra that allows communication between the swim bladder and the saccular otolith and increased sensitivity to sound. A similar simple otophysic connection has evolved independently in many groups of basal teleostean fishes, including some elopomorphs and clupeomorphs.

Eye Morphology and Vision

The eyes of both the Goldeye and Mooneye are large and the iris, particularly of the Goldeye, is golden in color. Direct studies of visual acuity are unavailable for either, but rods and cones are both present (Best & Nicol 1979; Braekevelt 1982a), despite reports that the retinas in these fishes lack cones (e.g., Moore 1944). Bundles of photoreceptors contain about equal number of cones and rods (of about 60 photoreceptors, 30 are cones; Best & Nicol 1979). This suggests that they are vision generalists (i.e., not adapted to dark or light environments exclusively). Both species of *Hiodon* have tapeta lucida (Moore 1944; Moore & McDougal 1949), and the reflectance of the tapeta is probably in part the root of their common names. The cells of the tapeta contain organelles with reflecting crystals formed primarily by uric acid (Zyznar et al. 1978), which is unusual, if not unique, among vertebrates (e.g., in other fishes tapeta lucida are formed by guanine crystals). Two types of reflecting crystals occur in the eye of Goldeye (Best & Nicol 1979), crystallites and rodlets, which reflect light slightly differently based on their structure and position (see also Braekevelt 1982ab). The presence of tapeta may be a specialization for life in turbid environment habitats (Goldeye) or possibly nocturnal habits (both the Goldeye and the Mooneye).

GENETICS

Although used as an exemplar basal teleost in broad molecular phylogenetic studies of actinopterygian evolution, the genetics of Hiodontidae are poorly studied. No studies of intraspecific or phylogeographic genetic variation are available for either species of *Hiodon*. Goldeyes contain at least eight *Hox* gene clusters, supporting the inferred fish genome duplication event at the origin of teleostean fishes (Crow et al. 2006; Chambers et al. 2009).

Karyology

The diploid complement of the chromosomes in *Hiodon* is 50 (Uyeno 1973), 8 of which are acrocentric or subtelocentric in *H. tergisus* (Beamish & Uyeno 1978; see also Vasil'yev 1980). Goldeyes are unique among osteoglossomorphs in having no acrocentric chromosomes (all are metacentric, submetacentric, 40; or subtelocentric, 10) (Uyeno 1973). The cellular DNA content of *Hiodon* ranges from 1.23×10^{-9} to 1.24×10^{-9} mg/cell (Beamish & Uyeno 1973).

PHYSIOLOGY

Few studies have focused on the physiology of *Hiodon*, and most aspects remain completely unstudied. The Goldeye and Mooneye are freshwater fishes, although precise levels of salt tolerance are unknown (Table 9.1). Oxygen consumption of Goldeyes fell during swimming (over a temperature range of 5–15°C), but consumption at rest was relatively constant (Hart 1968). The extensive latitudinal range of both species suggests a broad temperature tolerance at least among populations. Based on selection and avoidance of thermal zones in the Wabash and Cayuga Rivers, Indiana, optimal temperatures were about 27–29°C for both species (Becker 1983 citing Gammon 1973). Given the condition of habitats in which they occur, the two species are often contrasted as being tolerant (Goldeye) and relatively intolerant (Mooneye) of turbidity, but quantitative comparative data of effects of turbidity on the species are lacking.

Reproductive Physiology

Reproductive physiology has been examined in the Goldeye to a limited degree. In the final maturation of oocytes, the germinal vesicle migration and oil droplet formation (see reproductive section) are mediated by gonadotropins and progesterone (Pankhurst 1985). Both stages occur before ovulation as is usual in teleostean fishes. In a study of annual levels of gonadotropins and testosterone in the Goldeye, gonadotropin levels in females peaked in

June, corresponding to the spawning season (Pankhurst et al. 1986ab). As fish age, fat is stored in the gonads at a faster rate than in the gut, liver, or muscle, which suggests greater energetic cost for maintaining gonad structure and development (Craig et al. 1989).

Contaminants

Uptake and excretion of most heavy metals appear to be in equilibrium in muscle and ovary tissue in the Goldeye. Mercury, however, increases in concentration in muscle at a rate of 26.2 ng $g^{-1} year^{-1}$ over the life of the individual, and the mean concentration of mercury in ovaries was 7% that found in muscle (Donald & Sardella 2010).

BEHAVIOR

The Mooneye and Goldeye are thought to be fragile and difficult to keep or manipulate in laboratory and experimental settings. Nevertheless, individuals can live for 1–2 years in the laboratory (Fernet & Smith 1976; Hoover 2004). This fragility might preclude, for example, radio or acoustic telemetry techniques needed to better understand their behavior in nature. No telemetry studies of the behavior of *Hiodon* are available to date, and without such studies, behavioral observations in the wild likely will be difficult because both species of *Hiodon* live in open, often turbid environments.

Movement and Diel Activity

Hiodon make yearly migrations upstream in spring before spawning (see reproductive section). After spawning, fish continue moving upstream apparently to feed (Scott & Crossman 1973). In autumn, individuals migrate downstream to overwinter in deeper areas of lakes and rivers and are probably mostly inactive in winter. In Canada, Goldeye growth ceased in winter (Scott & Crossman 1973).

Both species, but particularly the Goldeye, are thought to be largely nocturnal or crepuscular in habits. During daylight, Mooneyes are taken frequently in deeper channels of rivers but may move to the shallows in the evening to feed (Roberts 1989). In one study, 75% of the oldest Goldeyes were taken in midwater trawls within 5 m of the surface at night (Becker 1983 citing Gasaway 1970). In Saskatchewan marshes, young Goldeyes moved most near sunrise and sunset, and activity was generally greater at night than during the day (Sprules 1947).

Territoriality and Dominance

Based on behavior of tank-held individuals from the Peace-Athabasca Delta, Alberta, Goldeyes may establish open-water territories (versus substrate-based territories, Fernet & Smith 1976). The position of the territory was not fixed in the observation tank, but it remained about the same size. Dominance was established between a pair of fish within a day of their introduction. Continued introduction of adults into the tank suppressed aggressive interactions between individuals, and after several such introductions, a schooling behavior was observed (which was perhaps caused by the small size of the experimental tank). Non-resident fish, females, and smaller individuals won more fights (i.e., encounters between pairs of fish) than resident fish, males, or larger individuals.

REPRODUCTION

Sexual Maturity

Males mature before females, but the age at maturity appears to vary between populations (Table 9.1). In the Red Lakes, Minnesota, mature male Goldeyes were ≥3 years old, and mature females were ≥4 years old (Van Oosten & Deason 1957; Grosslein & Smith 1959). In Lake Winnipegosis and the Saskatchewan River, both in Manitoba, Goldeye males matured at ages 4–7 and females matured at ages 5–9, but in Lake Claire, Alberta, males did not begin to mature until 6–9 years of age and females until 7–10 years (Kennedy & Sprules 1967). Mooneyes from the Assiniboine River, Manitoba, become sexually mature at 4–6 years old with males generally maturing 1 year before females (Glenn & Williams 1976). In Mooneyes from Lake Erie, fish 3–5 years old were mature (Van Oosten 1961).

Spawning Migrations

Both species of *Hiodon* are migratory spring spawners (April to June; Table 9.1). In the Peace River, northern Alberta, adult Goldeyes begin to move toward spawning grounds in the lakes of the delta (i.e., at its entrance into Athabasca Lake) in March, but they do not enter the delta until after ice breakup in May (Donald & Kooyman 1977a). Post-spawning upstream migrations begin in July and continue through mid-August. In this system, the complete spawning migration (i.e., migration from the wintering grounds to the delta spawning grounds and the subsequent return to the wintering grounds) might cover

≤800 km for some individuals, although tagging or telemetry studies have not confirmed such distances. In contrast, spawning of Mooneyes in the Red Deer River, Alberta, occurs in late May and June (temperatures >12°C), after an upstream migration in late April and May, followed by a subsequent downstream displacement of eggs and larvae (Roberts 1989). Geographic and taxonomic variation likely occurs in migration and spawning patterns that has yet to be described.

Spawning Habitat and Timing

Although not observed directly to date, spawning is thought to take place in midwater and at night (Kennedy & Sprules 1967). The substrate over which spawning takes place is unknown, although according to Wallus (1990b) both species spawn over rock and gravel as well as in turbid pools and backwaters (Goldeye) and swift clear waters (Mooneye). Goldeyes also spawn in shallow areas of lakes (Boschung & Mayden 2004), and eggs of Mooneyes were collected from near the tailwaters of dams (Wallus & Buchanan 1989). Timing of spawning for both species is variable across their ranges, and appears to be correlated with water temperature (Table 9.1). Mooneyes from the Assiniboine River, Manitoba, spawn between May and June at water temperatures of 10–13°C (Glenn & Williams 1976). Mooneyes in the Tennessee and Cumberland Rivers, Tennessee, spawn at 8–15°C; peak spawning occurs in late April and May (Wallus & Buchanan 1989). Goldeyes spawn in May and June at water temperatures of 10–13°C in Canada (Kennedy & Sprules 1967). Homing to particular spawning sites apparently does not occur in the Goldeye, but rather the location of spawning depends on local conditions and other environmental factors (Donald & Kooyman 1977a).

Spawning Behavior and Fecundity

Mature male *Hiodon* have a modified anal fin with a rounded anterior margin and increased musculature (Battle & Sprules 1960; Hilton 2002). The male is thought to cup its anal fin against the female during spawning, and the female and male both release their gametes into this cup. Males at the height of spawning have comparably little milt in their gonads, suggesting that some mechanism must conserve sperm during spawning, and the hypothesized cupping mechanism would do this (Kennedy & Sprules 1967; Pankhurst et al. 1986a).

Before spawning, the testes become reddish in color, and the ovaries fill the body cavity (Battle & Sprules 1960). Ripe eggs are steel blue in color and about 2 mm in diameter in Mooneyes, although slight latitudinal variation occurs in their size with more northern populations having smaller ova (1.98 mm diameter, Assiniboine River, Manitoba, Glenn & Williams 1976; 2.0–2.5 mm, Tennessee and Cumberland Rivers, Tennessee, Wallus & Buchanan 1989; 2.16–2.77 mm, Tallapoosa River, Alabama, Katechis et al. 2007; Table 9.1). Goldeyes from the Peace-Athabasca Delta, Alberta, do spawn annually, but those from the upper Peace River do not (Donald & Kooyman 1977a; Bishop 1974). Females may not spawn annually based on the observation of reproductively quiescent animals (Pankhurst et al. 1986a), but ages were not determined for the quiescent specimens, so these possibly were post-reproductive animals. In contrast to the gonads of many spring-spawning fishes, those of *Hiodon*, after a short period of shrinking immediately after spawning, grow substantially during the summer and reach 70–90% of the size for spawning by autumn (e.g., Glenn & Williams 1976; Pankhurst et al. 1986a). Although large in the fall, eggs do not ripen until just before spawning. Females lack an oviduct, and eggs are shed from the ovary directly into the body cavity, where they are expelled through a genital pore positioned just posterior to the anus (Kennedy & Sprules 1967). No difference in the size or maturity status of eggs from individuals on or near spawning grounds was found in the Mooneye, suggesting that the species releases the entire complement of mature eggs with each spawn (Katechis et al. 2007).

In a Manitoba population, Glenn & Williams (1976) estimated 5,000–9,000 mature eggs/female for a population of Mooneyes (relative fecundity of 2,000–2,400 eggs / 100 g of body weight). Similar fecundity (5,321–7,432 eggs/female) occurred in Mooneyes from the lower Tallapoosa River, Alabama (Katechis et al. 2007). In the Tennessee and Cumberland Rivers, Tennessee, fecundity of Mooneyes was 3,000–7,000 eggs/female (Wallus & Buchanan 1989). Fecundity estimates for Goldeyes range as high as 25,238 eggs/female (Kennedy & Sprules 1967), but most estimates are lower (average of 12,969 eggs/female, 15 individuals, 5 different lakes). Fecundity is related to both weight and age of the female. In the Assiniboine River (Manitoba), both total and relative fecundity for Mooneyes was lowest for first-year spawners (age 4), sequentially greater in second- to fifth-year spawners, and then declined after the fifth year (age 8) of spawning (Glenn & Williams 1976).

Egg and Larval Development

No post-spawning parental care occurs. The non-adhesive, semi-buoyant eggs possess an oil droplet, causing them to float in the water column, presumably drifting downstream from the spawning site (Battle & Sprules 1960; Table 9.1). The distantly related African Butterfly Fish, *Pantodon buchholzi*, is the only other osteoglossomorph known to have an oil droplet in the egg (Britz 2004). Fertilized eggs of the Goldeye are slightly larger in diameter (4.0 mm) than those of the Mooneye (3.3–3.9 mm; Wallus 1990b).

The embryology of *Hiodon* is poorly known (Battle & Sprules 1960). At the 41-somite stage, the developing embryo is wrapped around the egg about two-thirds of the diameter of the yolk. At this stage, the notochord is present, the brain is divided into three parts, the lens of the eye has developed, and the olfactory chambers are developing (Battle & Sprules 1960). By the 51-somite stage, the head has lifted free from the surface of the yolk as has the caudal region to about 10 somites anterior to the anus (Battle & Sprules 1960). In Goldeyes, hatching occurs in about 2 weeks (Scott & Crossman 1973; Wallus 1990b), although no laboratory rearing has occurred, and the correlation of developmental timing to water temperature is unknown.

The two species of *Hiodon* are similar in their larval and post-larval morphology (Fig. 9.5), differing in meristic and morphometric features that reflect differences in the adults of the species (e.g., ≥23 post-anal myomeres in Goldeye versus ≤23 in Mooneye). Both species of *Hiodon*

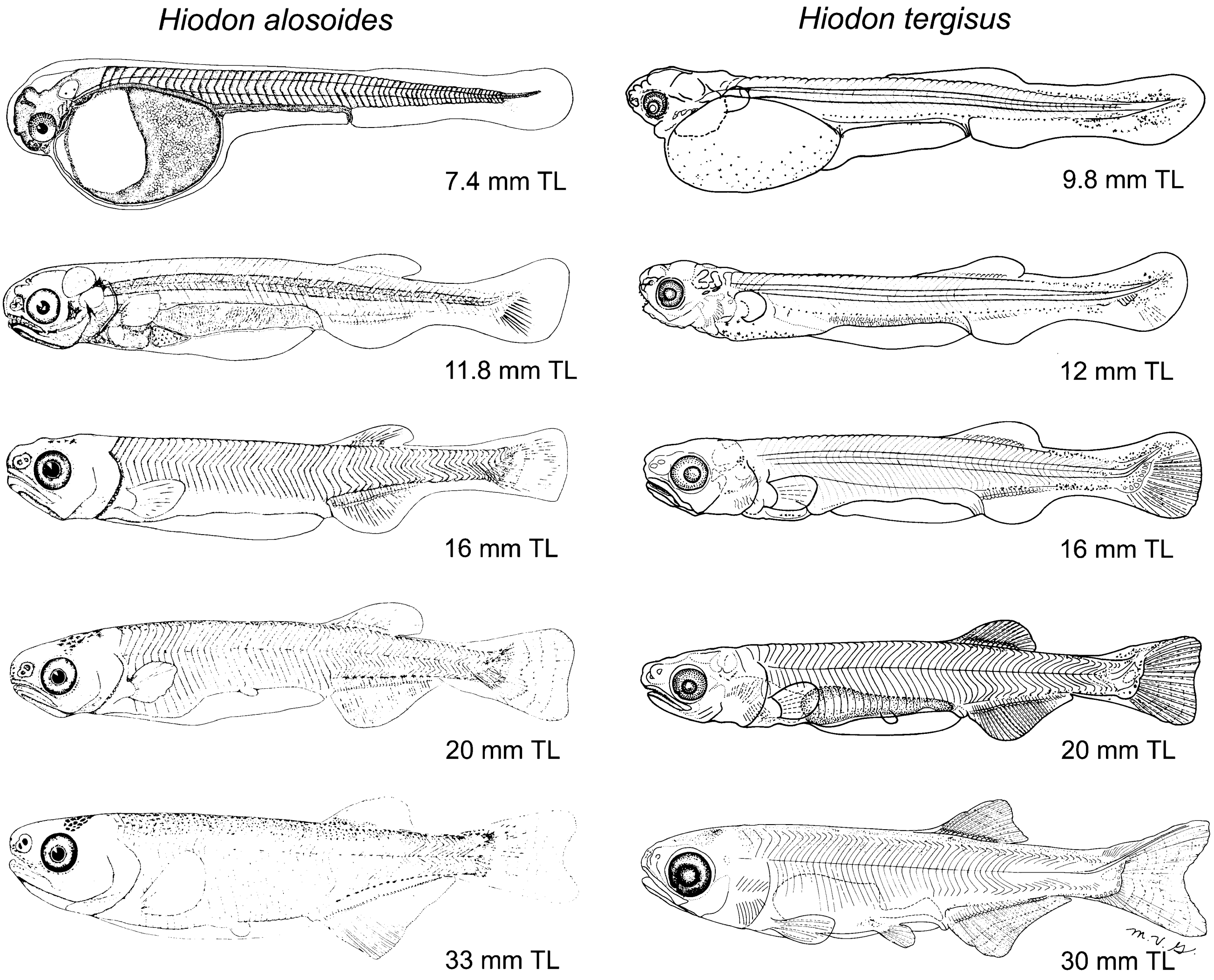

Figure 9.5. Early life history stages of Goldeye, *Hiodon alosoides*, and Mooneye, *Hiodon tergisus* (modified from Wallus 1990; used with permission of the Tennessee Valley Authority).

hatch at about 7 mm TL (smallest post-hatching specimens described: Mooneye, 7.1 mm TL, Snyder & Douglas 1978; Goldeye, 7.27 mm TL, Battle & Sprules 1960). At these early stages the embryos have a large oil globule in the yolk sac. The anterior position of this oil globule, which persists until after fin development, causes the larvae to drift vertically (i.e., with its head toward the surface of the water) at or near the surface of the water column (Battle & Sprules 1960). Early larval stages are largely unpigmented with the exception of the eye, and in Mooneyes, slight pigmentation at the base of the median fins in the caudal region. Pigmentation gradually increases through the post yolk-sac and juvenile stages. Median fin rays begin to form at about 13.0–13.5 mm TL. The pectoral fins begin to form at about this same time, but the pelvic fins do not develop until much larger sizes (e.g., 19–21 mm TL for Goldeye). The yolk sac is absorbed earlier in Goldeyes (16 mm TL) than in Mooneyes (21.5 mm TL); by the time the yolk sac disappears, the oral teeth are well developed. Body squamation is complete by 40 mm TL in Goldeyes and 44 mm TL in Mooneyes (Wallus 1986b, 1990b).

ECOLOGY

Habitat

Both species of *Hiodon* inhabit slow-moving, turbid environments, including large rivers, lakes, ponds, and adjacent swamps (Kennedy & Sprules 1967; Roberts 1989) with some evidence that they frequent rivers more often than other habitats (i.e., oxbows and reservoirs) (Etnier & Starnes 1993; Ross 2001). Both species occur in turbid waters (Roberts 1989), but Mooneyes more typically inhabit clear rivers (e.g., Etnier & Starnes 1993) and are considered less tolerant of turbid waters than are Goldeyes (Trautman 1957).

In Fort Peck Reservoir, Montana, Goldeyes congregate near the surface in the summer and early autumn. From late autumn to spring, when surface temperatures were between 1.1 and 8.9° C, they were at depths between 2.4 and 9.8 m. Although correlated to surface water temperature, this vertical distribution was likely due to tracking of prey abundance (Cooper 1973).

Abundance

Mooneyes and Goldeyes can be locally abundant. For example, along two 16 km segments of the channelized Missouri River, Nebraska, a mark-recapture study in winter provided conservative population estimates with confidence intervals ranging between 1,524 and 11,568 Goldeyes (Hesse & Newcomb 1982). Trawling in the upper Mississippi River (Pool 26), adjacent to Illinois, yielded estimates of 3.32 individuals/ha and 0.24 individual/ha for Mooneyes and Goldeyes, respectively. Mooneyes were encountered primarily in autumn and early winter and Goldeyes year round (Dettmers et al. 2001). Year-class strength may depend on environmental factors during early life history stages (i.e., years with warm, calm weather produce stronger year-classes; Donald 1997). In the Peace-Athabasca Delta, Alberta, a dominant year-class may only occur <2 times/decade (Donald & Aitken 2005). Moon et al. (1998a), however, concluded consistent recruitment occurred in their study population, but their sample included only six year-classes.

Diet

As generalist predators, hiodontids eat an array of prey items, including many types of crustaceans (amphipods, decapods), insects (corixids, coleopterans, ephemeropterans, dipterans, odonates, plecopterans, and hymenopterans), other fishes (*Esox* spp., cyprinids, percids, gasterosteids), frogs, and small mammals. The composition of their diet reflects locally abundant prey species (Kennedy & Sprules 1967; Scott & Crossman 1973; Glenn 1975b). They appear to feed primarily at dusk and dawn, although gut contents including noctuid moths and other nocturnal prey suggests that feeding may also be nocturnal. The inclusion of terrestrial insects in the diet suggests they also surface feed (Bajkov 1930; Grosslein & Smith 1959; Kennedy & Sprules 1967), although stomachs of young Mooneyes contained aquatic larval and pupal stages of insects, suggesting young individuals may not feed at the surface (Glenn 1978). Hiodontid larvae feed primarily on calanoid copepods and cladocerans, but older fish (e.g., post-larval and young-of-the-year) shift to corixids and other insects as well as other larger prey. Seasonal and annual shifts in diet likely represent shifts in prey abundance. *Daphnia magna* was an important component of the diet of Goldeyes from the Peace-Athabasca Delta, Alberta, in a year in which the crustacean was particularly abundant but was absent in the diet in the next two years when *Daphnia magna* were relatively scarce, suggesting that *Hiodon* is not tied to particular prey but more likely seeks out particular prey sizes (Donald & Kooyman 1977b). Peak relative abundance of adult Goldeyes and larval fishes, however, coincided in backwaters of the Missouri River, but Goldeyes did not appear to feed significantly on larval fishes (2.5% prey by occurrence and <0.1% prey by number, Moon et al. 1998b).

Age and Growth

The maximum recorded length of the Mooneye (445 mm TL) is slightly shorter than that of the Goldeye (508 mm TL; Trautman 1957). The world angling records are a 1.7 kg Goldeye angled in South Dakota and a 0.68 kg Mooneye caught in Minnesota (IGFA 2006). Most large Goldeyes and Mooneyes, however, are ≤0.7 and 0.35 kg, respectively (summary by Carlander 1969).

Significant latitudinal variation exists in the growth rate of *Hiodon*, and more northern populations apparently experience slower growth (Table 9.2; Kennedy & Sprules 1967; Scott & Crossman 1973). For both Goldeye and Mooneye populations in Quebec, individuals from more northerly populations (Matagami Lake, on the Nottaway River, James Bay drainage) had significantly slower growth than individuals from farther south but had greater longevity and equal maximum sizes (Hazel et al. 1983). In contrast, Mooneyes from the Tallapoosa River, Alabama, grew faster than the population in Assiniboine River, Manitoba (data from Glenn 1975a), although this result possibly was skewed because the Tallapoosa sample consisted of fewer and larger fish and thereby overestimated the growth rate (Katechis et al. 2007).

Greatest growth increments occur in the first year of growth in *Hiodon*. In the Assiniboine River, Manitoba (Glenn 1975a, 1976, 1978), Mooneyes reached about 160 mm TL (24 g) during the first summer of growth with 90% of the growth achieved by the end of August (Glenn 1978). In the first summer of growth for the Goldeye population in the Saskatchewan River, maximum growth rates occurred during late July and early August (reaching 80 mm TL by 20 August), and little growth occurred after September (Fig. 9.6A; Kennedy & Sprules 1967). Similarly, from back-calculated mean length-at-age, the greatest growth increment occurred in year 1 for a population of Goldeyes from the Missouri River, North Dakota

Table 9.2. Mean length (mm) at age (in years) for various populations of Goldeye, *Hiodon alosoides* (—, no data).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Total length															
[1]Lake Oahe, South Dakota	114	207	261	298	321	336	347	—	—	—	—	—	—	—	—
[2]Missouri River, North Dakota	122	189	234	276	298	305	315	—	—	—	—	—	—	—	—
[2]"Northern waters"	79	175	198	259	290	302	338	—	—	—	—	—	—	—	—
Fork Length															
[3]Lake Winnipegosis, Manitoba (female)	—	183	221	274	—	315	345	325	—	—	—	—	—	—	—
[3]Lake Winnipegosis, Manitoba (male)	—	158	218	264	297	302	305	315	—	—	—	—	—	—	—
[3]Saskatchewan Delta, Manitoba (female)	158	213	257	287	305	325	340	351	361	394	368	432	—	—	—
[3]Saskatchewan Delta, Manitoba (male)	165	211	252	279	297	312	328	335	353	368	—	—	—	—	—
[3]Lake Claire, Alberta (female)	69	132	178	211	254	264	305	335	348	376	386	389	406	437	—
[3]Lake Claire, Alberta (female)	69	137	178	208	234	262	307	333	351	363	368	368	361	—	—
[3]Sandy Lake, Ontario (female)	—	—	—	—	—	264	290	279	302	310	305	—	—	335	368
[3]Sandy Lake, Ontario (male)	—	—	—	—	241	259	285	285	292	297	300	302	310	305	—

[1] Miller & Nelson (1974).
[2] Moon et al. (1998a).
[3] Kennedy & Sprules (1967).

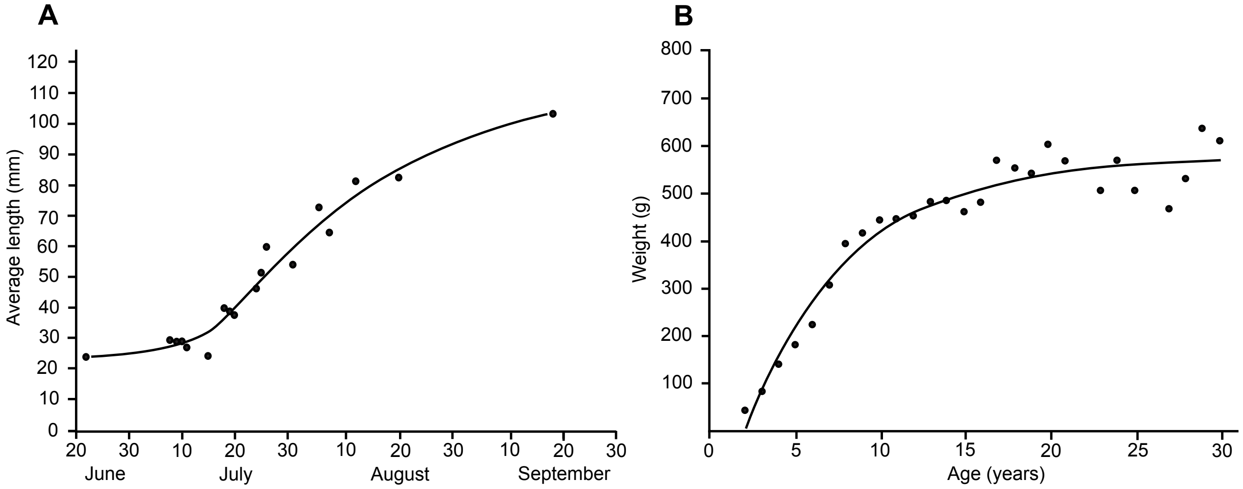

Figure 9.6. Growth patterns for Goldeye, *Hiodon alosoides*. (A) Growth rate during the first summer of life for the Saskatchewan River population (redrawn from Kennedy & Sprules 1967). (B) Von Bertalanffy growth curve for the Peace-Athabasca Delta population ($\text{weight} = 570 \cdot [1 - e^{-0.16(\text{age}-1.94)}]$; n = 1,261) (redrawn from Donald & Aitken 2005).

(Moon et al. 1998a). Growth rates decreased by 50% in year 2, slightly more in year 3, and then remained relatively constant in years 4–7.

Sexual dimorphism occurs in the growth rates in older Goldeyes (3–9 years old), with males growing slower than females (Kennedy & Sprules 1967). This sexual dimorphism varied between populations; although it was not associated with maturity, this relationship is based on weight-at-age, and so bias may be associated with reproductive condition.

In the upper Peace River, Alberta, Goldeyes were smaller-at-age than individuals from the Peace-Athabasca Delta. The Goldeyes from the Delta population were also larger in the early 1970s than were individuals sampled from the same population in the 1940s. This difference may have resulted from heavy exploitation from a fishery in the region between 1948 and 1966. The thinned post-fishery population may have experienced decreased competition for food resources and displayed higher growth rates (Donald & Kooyman 1977a).

The mortality rate was nearly 100% for 14-year-old fish (both males and females, aged by scales) in populations from Manitoba and Alberta (Kennedy & Sprules 1967), suggesting this is the maximum age for Goldeyes. Nevertheless, a 30-year-old (607 g) individual (opercle-aged) occurred from the Peace-Athabasca Delta system (Donald & Aitken 2005; Table 9.1; Fig. 9.6B). Mooneyes grow slower than Goldeyes and likely do not live >8 years (Van Oosten 1961; Boschung & Mayden 2004), although a 12-year-old specimen was based on counts of annuli in vertebral centra (Newbrey et al. 2007). In the latter study, growth rates also were estimated for fossil specimens recovered as isolated centra from the Late Cretaceous Dinosaur Park Formation. The estimates suggested the presence of two hiodontid taxa in this formation, both of which had slower growth rates than either extant Goldeye or Mooneye. Most aging studies of extant Mooneye and Goldeye are based on estimates derived from annuli counts read from scales that are consistently lower or less reliably read than annuli from opercles or otoliths (Donald et al. 1992; Katechis et al. 2007). Verification of any age methods (i.e., validation of annual formation of annuli) through mark-recapture studies has yet to be performed.

Parasitism and Predators

Parasites of *Hiodon* include cestodes, trematodes, acanthocephalans, nematodes, and crustaceans (Self 1954; Kennedy & Sprules 1967; Scott & Crossman 1973; Hoffman 1999; Choudhury & Nelson 2000). In the Assiniboine River, Manitoba, 85% of Goldeyes are infected with the nematode *Cystidicoloides tenuissima* and/or the flukes *Paurorhynchus hiodontis* and *Crepidostomum hiodontos*, though young-of-the-year had lower infection rates (45–74%). Parasitism rates were also generally lower in the winter months than in the summer (Glenn 1980). The unionid bivalve *Amblema plicata* infests Mooneyes, although its metamorphosis on that species has not been recorded (Weiss & Layzer 1995).

Predatory sympatric fishes such as Pikes (*Esox* spp.) and Walleye (*Sander vitreum*) feed on *Hiodon*. In addition, birds (e.g., cormorants) and mammals may also prey on *Hiodon* (Kennedy & Sprules 1967).

CONSERVATION

Neither species of *Hiodon* is federally protected in the United States or Canada. Even so, the ranges of both appear to be shrinking, particularly at their edges, and they are considered Threatened or of Special Concern in several states in which they occur (Table 9.1). This is especially true of the Mooneye. For example, the Mooneye formerly occurred in Lake Michigan but now is apparently extirpated from that water body (NatureServe 2009). The apparent shrinkage in range is not a recent occurrence. Decline of the Goldeye in the commercial fisheries of Minnesota was apparent during the first half of the 1900s (Grosslein & Smith 1959). The decline of the Mooneye in the Ohio River was suggested to be correlated with increased turbidity (Trautman 1957). Roberts (1989:140) suggested, however, that turbidity may be "the most visible, but not the only change that occurred in Ohio."

Across their range both species are of concern in a number of states. Goldeyes have virtually disappeared from the upper Tennessee and Cumberland Rivers following their impoundment (Etnier & Starnes 1993). Goldeyes are considered Extirpated in Alabama, Critically Imperiled in Ohio and West Virginia, and Imperiled in Pennsylvania, Illinois, Wisconsin, Arkansas, and Wyoming; populations in Texas, Quebec, Ontario, and British Columbia are Vulnerable. Mooneyes are considered Critically Imperiled in New York, North Carolina, and Georgia and imperiled in Pennsylvania, Michigan, and Illinois; populations in West Virginia, Alabama, Arkansas, Missouri, Oklahoma, Texas, Alberta, and Saskatchewan are Vulnerable (NatureServe 2009).

COMMERCIAL IMPORTANCE

Most commercial fishing for *Hiodon* occurs in Canada, and the fishery for the Goldeye (marketed as Winnipeg Goldeye) may have caused decline in some populations. Kennedy and Sprules (1967:35) considered the marketing of Winnipeg Goldeye to be "the triumph of art over nature. Its characteristic color [in the market] results from an aniline dye. Its characteristic taste is essentially that of oakwood smoke. Its texture can be improved by freezing. Its name is derived from a lake where it is no longer caught in appreciable quantities." The tasteless aniline dye was used to color the skin, but not the flesh, and simulated the color obtained from wood smoke, which faded with storage (Scott & Crossman 1973). Scott & Crossman (1973:331), who quoted Kennedy & Sprules, echoed their sentiment, and wrote that the "taste of fresh Goldeye was said to be insipid, muddy, and like that of salted brown paper." Of course, taste is a matter of opinion. Jordan & Thompson (1910:353) wrote that when the Goldeye is "smoked, it is fairly to be called delicious, and as a panfish, although beset by small bones, its flesh is excellent, scarcely inferior to that of the whitefish. It is flaky, rather firm, and of good quality."

The decline of the Goldeye in the commercial catch of the Red Lakes of Minnesota during the first half of the 1900s was correlated with an increase in effort in this fishery (Grosslein & Smith 1959). Although there was some commercial interest for Goldeyes in Canada in the late 1800s, a directed commercial gillnet fishery did not become well established until after 1911. Annual catches in Canada exceeded 453.59 mt (1 million pounds) by 1926, but after 1931 the catch declined to 81.65 mt (180,000 pounds) in 1965 (Scott & Crossman 1973). In 2003 landings of the Goldeye in Canada (predominantly from Manitoba, but also from Saskatchewan, Alberta, and the Northwest Territories) totaled only 8 mt (17,637 pounds) live weight, and had a value of C$19,000 (FOC 2010). Mooneyes apparently were never exploited commercially to any significant degree. Both species are said to provide good sport on light tackle.

LITERATURE GUIDE

Important reviews and studies of the biology of *Hiodon* include Kennedy & Sprules (1967) and Donald & Kooyman (1977a). Beyond references cited previously, particularly useful reviews of the biology of *Hiodon* appear in Trautman (1957), Scott & Crossman (1973), and Beckett (1983).

Acknowledgments

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Chapter 10

Anguillidae: Freshwater Eels

Alex Haro

Given their unique life history, ecology, adaptations, migrations, and behaviors, anguillid Eels, or Freshwater Eels (Anguillidae: Anguilliformes, Eels), comprise perhaps one of the most familiar, common, geographically widely dispersed, yet enigmatic and poorly understood groups of fishes. The family name Anguillidae is formed from the Latin root for Eel and is related to "anguis," snake (Boschung & Mayden 2004). Their simple and familiar snakelike body plan, nondescript coloration, and cryptic habits belie a complex and fascinating life history and evolutionary past. Although significant gains in understanding of the biology of Anguillidae have recently been achieved, new findings continue to surprise investigators, and Schmidt's (1912:636) quote still rings true more than a century later: "altogether, the whole story of the eel . . . has come to read almost like a romance, wherein reality has far exceeded the dreams of phantasy."

Anguillid Eels are catadromous and generally have a significant freshwater and oceanic migration of adults to a localized spawning area in the open ocean. The nature of the migration and location of marine spawning areas were largely unknown until recently. Likewise, drift of larvae from the open ocean back to coastal habitats is extensive, both temporally and spatially, raising questions about the adaptation and evolution of this protracted larval stage. The laterally compressed, nearly transparent leptocephalus larva is a life history attribute shared with other elopomorph fishes such as Tarpons (Megalopidae) and Bonefishes (Abulidae). The freshwater phase of the life history of anguillid Eels involves tremendous variability in age, growth, sex determination, and behavior, likely influenced largely by the environment. In addition, anguillid Eels may be found in practically every freshwater and coastal marine aquatic habitat.

The American Eel, *Anguilla rostrata*, is the sole anguillid species in North America. Its biology is quite similar to that of other species of temperate anguillids, and much of what is known about other well-studied species of *Anguilla* (e.g., primarily the European Eel, *Anguilla anguilla*, and to a lesser degree the Japanese Eel, *Anguilla japonica*), can for the most part be applied to *A. rostrata*, but some exceptions exist. Here the term "anguillid Eel" is used in context with aspects of biology determined for the other similar anguillid Eel species that are assumed to be applicable to *A. rostrata*, but statements here regarding the American Eel are specific to studies of *A. rostrata*.

The life history and migration cycle of the American Eel is important to this review and can be summarized briefly (Fig. 10.1; Table 10.1). American Eels spawn in the open ocean of the Sargasso Sea (North Atlantic Gyre) in a poorly defined area spanning about 5 degrees of latitude and 15 degrees of longitude (McCleave 2003). Eggs and developing leptocephalus larvae drift westward and northward in

Plate 10.1. American Eel, *Anguilla rostrata*

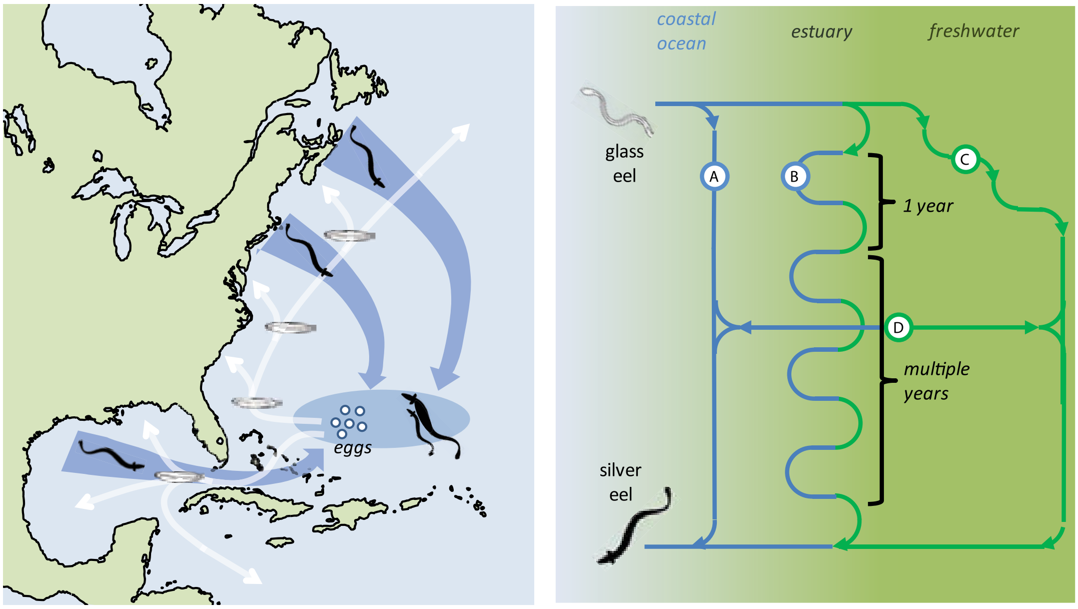

Figure 10.1. Left: Lifecycle of the American Eel, *Anguilla rostrata*, showing approximate spawning area in the Sargasso Sea, entrainment of eggs and leptocephalus larvae (Fig. 10.5) in the Gulf Stream and into the Gulf of Mexico (white arrow paths) toward coastal areas, and return migration of adult silver-phase eels to the Sargasso Sea (blue arrow paths). Arrows indicate general directions of movement and not necessarily actual oceanic paths of migration. *Right*: General description of regular and irregular migrations of juvenile and subadult American Eels within and between coastal and freshwater habitats: (A) occupation of coastal marine habitats without entry into fresh water; (B) regular seasonal annular movements between estuary and freshwater environments; (C) wholly freshwater existence, with continued movements into upstream habitats; (D) irregular movement between coastal, estuarine, or freshwater habitats during some point of the yellow-growth phase.

surface currents and are generally entrained into the Gulf Stream. Leptocephali feed, grow, and develop for about a year before metamorphosing into semi-pigmented juveniles, termed “glass Eels,” and gradually move coastward, entering whatever nearshore habitats, estuaries, and freshwater bodies to which ocean currents carry them, over a geographic range from northern South America to Greenland. Many glass Eels migrate into fresh water, but some remain in marine habitats; all begin to feed and grow and assume the familiar anguillid Eel morphology and coloration; they are termed “elvers” at smaller sizes and “yellow phase” at larger sizes (usually after 1 year within coastal environments). Juvenile anguillid Eels can invade a wide variety of lentic and lotic freshwater habitats and may migrate hundreds of kilometers upstream over many years. After several years in coastal and freshwater habitats, yellow-phase individuals metamorphose into the silver phase and migrate back to the ocean to begin their journey back to the Sargasso Sea, but this maturation and migration phase usually does not occur until Eels are at least 5–7 years of age and may not occur until individuals are decades old. Migrant adult American Eels may be ≤43 years old (Jessop 1987; Casselman 2003; Cairns et al. 2008) and possibly older. Upon reaching the ocean, silver-phase American Eels presumably swim to the Sargasso Sea over a 2- to 8-month period. Rates, depths, and routes of the oceanic spawning migration are unknown; after spawning, adult anguillid Eels presumably die. Although no adult American Eels have been captured or observed in the spawning area, it is the only location where the smallest and youngest larvae have been encountered, and thus it is likely the sole spawning area for the American Eel.

DIVERSITY AND DISTRIBUTION

The genus *Anguilla* consists of about 18 species, with several subspecies, distributed globally in tropical, subtropical, and temperate habitats (Aoyama 2009). Both the American Eel (*A. rostrata*) and the European Eel (*A. anguilla*) spawn in the

Table 10.1. Life history table for the American Eel, *Anguilla rostrata* (Anguillidae), in North America.

Trait	Description	References
Number of extant species	One	Lesueur 1817b
Strictly freshwater (ppt)	No; larval and silver phases fully marine; yellow phase may occur in marine environments	Kleckner & McCleave 1985; Barbin et al. 1998; Morrison 2003
Maximum size recorded in length and weight	115.9 cm TL; 3,340 g	Tremblay 2009
Maximum age	Males, 16 years; females, 43 years	Jessop 1987; Oliveira 1999; Casselman 2003; Cairns et al. 2008
Age and size at first reproduction	Males: 4–16 years; 22.8–39.8 cm TL Females: 6–43 years; 40–115.9 cm TL	Oliveira 1999; Casselman 2003; Able & Fahay 2010
Iteroparous or semelparous	Semelparous	Facey & Van den Avyle 1987
Fecundity estimates (ovarian counts)	Chesapeake Bay, 0.4 to 2.5 million; Maine, 1.84 to 19.92 million	Wenner & Musick 1974; Barbin & McCleave 1997
Mature egg diameter	960–1030 um	Oliveira & Hable 2010
Egg deposition sites	Open ocean, pelagic; presumably within upper 1,000 m	Kleckner et al. 1983; McCleave & Kleckner 1985
Clutch size	Unknown	Oliveira & Hable 2010
Range of nesting dates and temperatures	February and March; temperature unknown but probably between 16 and 24°C	McCleave 2003
Habitat of spawning sites; average water depth	Open ocean, pelagic; presumably within upper 1,000 m	Kleckner et al. 1983; McCleave & Kleckner 1985; Castonguay & McCleave 1987
Incubation period; larval type at hatching	3–4 days at 20°C; pre-leptocephalus stage	Miller 2009; Oliveira & Hable 2010
Mean size at hatching and swim-up	2.7 ± 0.2 mm TL	Oliveira & Hable 2010
Parental care	Presumably broadcast spawning with no parental care	Sorensen & Winn 1984
Major dietary items (adults)	Aquatic macroinvertebrates, small fish, carrion, fish eggs	Smith & Saunders 1955; Godfrey 1957; Able & Fahay 2010
General year-round habitat	Clear, small, unproductive headwater streams; large, turbid, productive mainstem rivers; blackwater swamps and rivers; subterranean springs and caves; clear and turbid, deep and shallow, vegetated and barren lakes and ponds; and fresh, brackish, and saltwater marshes, coastal marine habitats	Helfman et al. 1987
Migratory or diadromous	Diadromous (facultative catadrome)	Tsukamoto et al. 1998; Secor 1999; Jessop et al. 2006; Lamson et al. 2006
Imperilment status	Population at historic low; local abundance variable; of management concern; petitioned for federal listing as Endangered	Castonguay et al. 1994; Haro et al. 2000; MacGregor et al. 2008, 2009

Sargasso Sea in the Western North Atlantic. Both were considered conspecific as *A. anguilla* until *A. rostrata* was distinguished by its significantly lower vertebral count (103–110) compared with that of *A. anguilla* (110–119; Lesueur 1817b). Anguillidae is represented only by the American Eel in coastal and fresh waters of North America. There is no evidence for subspecies or polytypy within *A. rostrata*.

The continental range of American Eels spans from southern Greenland (although European Eel hybrid forms may be found in Iceland, Avise et al. 1990), eastern Labrador, Newfoundland, and Quebec, southward through the Canadian Maritimes, the eastern United States, the Gulf of Mexico, eastern Mexico, and along the Atlantic Coast of middle and central America as far south and east as Guyana (Fig. 10.2; Tesch 2003). American Eels also occur in coastal and freshwater habitats in Bermuda and throughout the Caribbean. Due to the general entrainment and northward drift of leptocephali via the Gulf Stream,

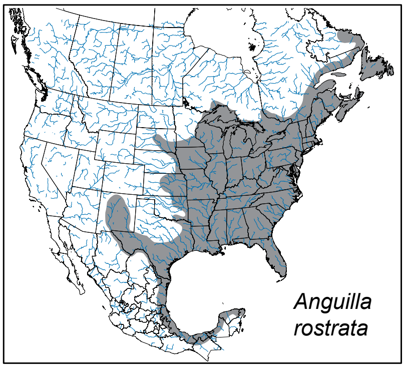

Figure 10.2. Freshwater range of the American Eel (shaded area), *Anguilla rostrata*, in North America. Range also extends north to Greenland and south to northern South America, Bermuda, and the Caribbean. Range also includes coastal marine habitats adjacent to the freshwater range. Widespread occurrence of the American Eel in the Great Lakes and their associated tributaries upstream of Lake Ontario may have been facilitated by invasion via the Welland Canal, extending between Lake Erie and Lake Ontario.

recruitment and abundance of American Eels south of Florida is typically lower than in more northerly locations.

Although previously thought to occupy primarily freshwater habitats, significant numbers of American Eels can spend most or all of their lifetimes in marine or estuarine habitats (Morrison et al. 2003) or regularly or irregularly (Lamson et al. 2006) migrate between marine and freshwater environments (Fig. 10.1). Thus, the American Eel and other anguillid Eels may be more properly thought of as facultative catadromes, and do not necessarily have to enter fresh water to successfully complete their lifecycle (Tsukamoto et al. 1998). American Eels that do enter fresh water may return to marine environments at almost any point in their growth phase to continue growth and maturation (Jessop et al. 2006).

Nonetheless, the vast majority of the post-larval American Eel population probably does volitionally enter fresh water as evidenced by upstream migrations of large numbers of juvenile glass Eels and elvers in the spring and

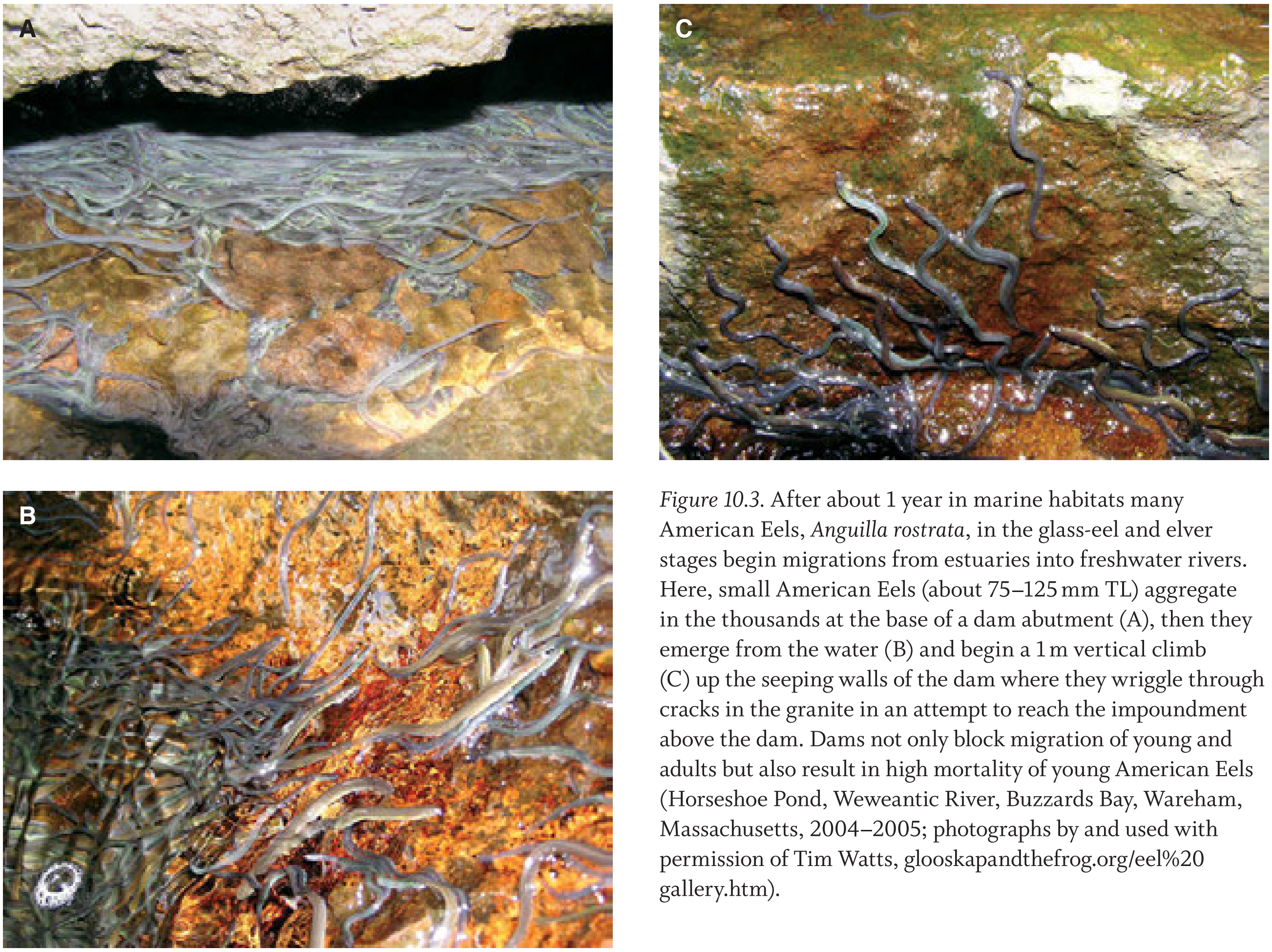

Figure 10.3. After about 1 year in marine habitats many American Eels, *Anguilla rostrata*, in the glass-eel and elver stages begin migrations from estuaries into freshwater rivers. Here, small American Eels (about 75–125 mm TL) aggregate in the thousands at the base of a dam abutment (A), then they emerge from the water (B) and begin a 1 m vertical climb (C) up the seeping walls of the dam where they wriggle through cracks in the granite in an attempt to reach the impoundment above the dam. Dams not only block migration of young and adults but also result in high mortality of young American Eels (Horseshoe Pond, Weweantic River, Buzzards Bay, Wareham, Massachusetts, 2004–2005; photographs by and used with permission of Tim Watts, glooskapandthefrog.org/eel%20gallery.htm).

summer months (Fig. 10.3). Although the primary distribution of post-larval American Eels is along the Atlantic Coast, this species can reach habitats far inland over the course of several years of upstream migration, and inland distribution of American Eels can extend hundreds of kilometers, reaching as far as the Great Lakes via the St. Lawrence River system (and into the upper Great Lakes via the Welland Canal) and into the upper Mississippi River system as far north as South Dakota (Fig. 10.2). Densities of American Eels in upper reaches of these large river systems are typically low, however, and density in general tends to decrease with distance upstream, due to attrition with age, barriers to movement, and cessation of upstream migration behavior after the first few years in fresh water (Haro & Krueger 1991; Smogor et al. 1995).

Non-Native Distribution

American Eels are reported from a variety of nonindigenous midwestern and western locations, all likely from purposeful or unintentional human translocation activities, including likely ballast water introduction (northern Lake Superior); aquaculture escapes (California and San Luis Valley, Colorado); intentional stocking (Sacramento and San Francisco Bays; Calumet River, Illinois; Lake Erie; Utah and Salt Lakes, Utah; Fox River, Wisconsin); and accidental release (Elkhorn River, Nebraska) (Fuller & Nico 2011).

PHYLOGENETIC RELATIONSHIPS

Anguillidae is considered the extant sister-group to all other living Anguilliformes (Forey et al. 1996), although the relationships among families of anguilliform Eels are not well understood due in part to their extreme diversity and reductive morphology (Nelson 2006). Species of *Anguilla* are difficult to separate based on morphological characters alone, although morphological classifications (Ege 1939; Wantanabe 2003) are largely supported by molecular methods (Aoyama & Tsukamoto 1997; Minegishi et al. 2005). Mitochondrial DNA analyses identified three major groups of *Anguilla*: an Indo-Pacific group, an Oceanian group, and an Atlantic group of which *A. rostrata* and *A. anguilla* comprise the sole species and a common node as sister-groups (Fig. 10.4; Minegishi et al. 2005).

Anguillid Eels have an evolutionary history spanning from 40 to 70 million years (Aoyama et al. 2001) and are thought to be marine and tropical in origin (Indo-Pacific; Ege 1939; Eckman 1953). Expansion of oceanic migratory loops of the leptocephalus larva to adult phase likely resulted in expansion of ranges into temperate habitats and provided a mechanism of speciation via creation of new migratory loops that have produced reproductively isolated populations within separate ocean circulation systems (Tsukamoto et al. 2002). The Atlantic species likely

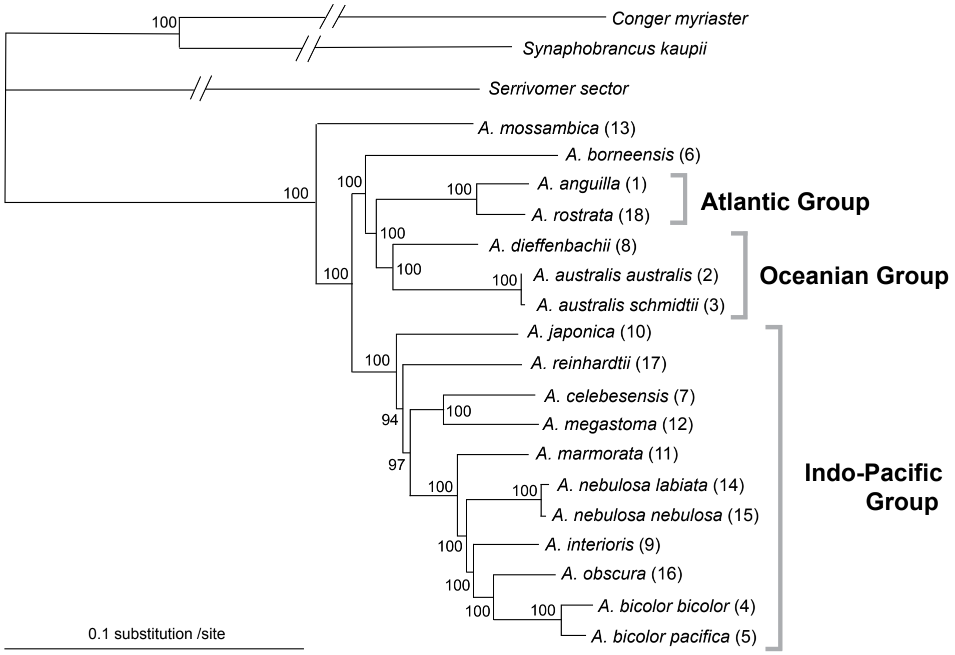
100
Conger myriaster
Synaphobrancus kaupii
Serrivomer sector
A. mossambica (13)
A. borneensis (6)
A. anguilla (1)
A. rostrata (18)
Atlantic Group
A. dieffenbachii (8)
A. australis australis (2)
A. australis schmidtii (3)
Oceanian Group
A. japonica (10)
A. reinhardtii (17)
A. celebesensis (7)
A. megastoma (12)
A. marmorata (11)
A. nebulosa labiata (14)
A. nebulosa nebulosa (15)
A. interioris (9)
A. obscura (16)
A. bicolor bicolor (4)
A. bicolor pacifica (5)
Indo-Pacific Group
94
97
0.1 substitution /site

Figure 10.4. Phylogenetic relationships of all currently recognized species of *Anguilla* and three outgroup species as determined by the entire mtDNA genome. Numerals beside the internal branches are Bayesian posterior probabilities (shown as percentages) (redrawn from Minegishi et al. 2005).

gained access to the proto–Atlantic Ocean from their Pacific Ocean ancestors early in the Tertiary (Lecomte-Finiger 1994), before the closure of the Tethys Sea about 30 mya (Aoyama 2003).

FOSSIL RECORD

A putative fossil specimen of *Anguilla* is described from the Messinian (Tertiary Piedmont Basin, northwestern Italy, Late Miocene, 11.2–5.3 mya), supposedly a juvenile (Sturani 1973). This specimen, however, was identified as *Anguilla* based primarily on number of vertebrae. Three fossil species of *Anguilla* are described from European deposits based on otolith morphology (Nolf 1985): †*A. annosa* (Early Eocene, 55.8–48.6 mya; England); †*A. rectangularis* (Middle Eocene, 48.6–37.2 mya; Belgium); and †*A. rouxi* (Oligocene, 33.9–28.4 mya; Belgium).

MORPHOLOGY

Anguillid Eels change dramatically in morphology concomitant with transitions among life stages. They have an unusually large (reaching ≤70 mm TL in *A. rostrata*) and long-lived leptocephalus larva that is generally unpigmented, leaf-shaped, and highly laterally compressed (Fig. 10.5). Leptocephali appear adapted to a lengthy pelagic existence in the open ocean, and although their metabolism is low and growth is generally slow, they have well-developed eyes, possess relatively large teeth, and appear to be active predators. Upon metamorphosis from the leptocephalus larva to the glass-Eel phase, the body becomes less laterally compressed and more rounded in cross section. Upon entering coastal waters, glass Eels rapidly recruit chromatophores along the vertebrae, head, and dorsal surfaces and chromatophores then develop laterally

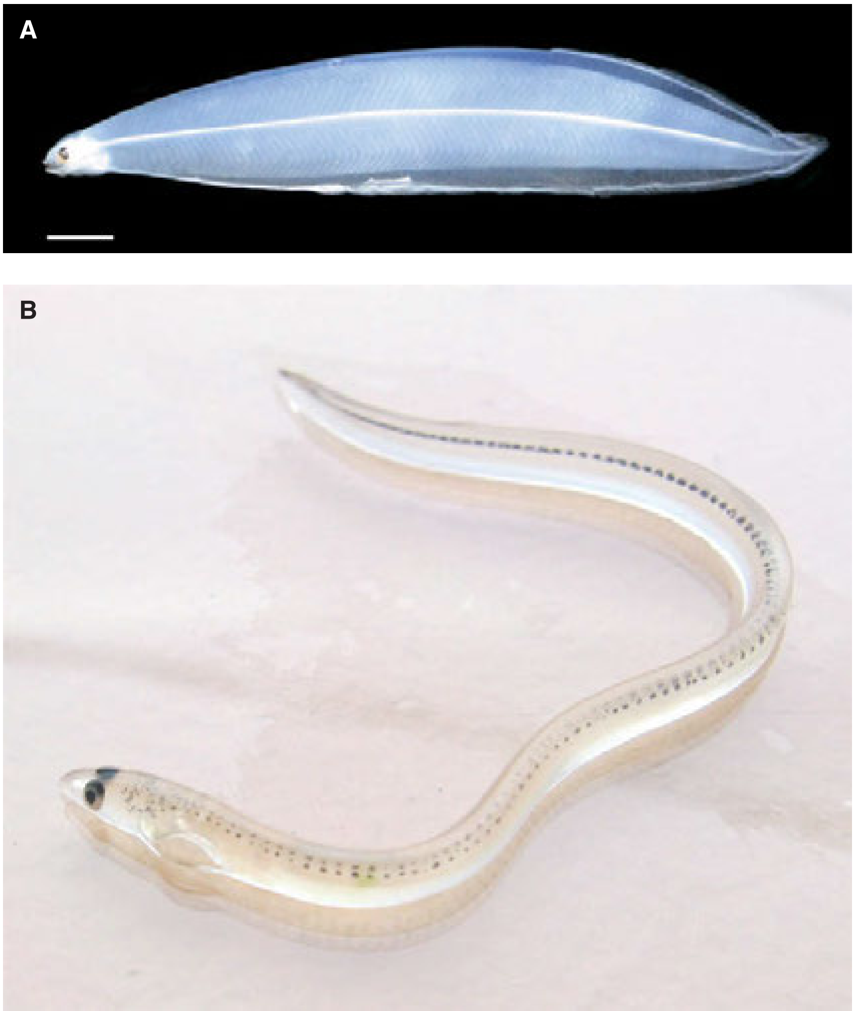

Figure 10.5. (A) Leptocephalus larva of the American Eel, *Anguilla rostrata*, captured from the Sargasso Sea; about 59.9 mm TL, bar = 5 mm (photograph courtesy and used with permission of M. Miller, Ocean Research Institute, University of Tokyo). (B) Glass-eel phase of *A. rostrata*, with vertebral and cranial pigmentation but dorsal and lateral dermal pigmentation undeveloped (photograph courtesy and used with permission of G. Verrault, Quebec Ministry of Natural Resources).

and ventrally (Fig. 10.5). Development of pigmentation stages is characterized in *A. anguilla* (Strubberg 1913; Bertin 1956) and *A. rostrata* (Haro & Krueger 1988). Black or brown dermal melanophores develop anteriorly and dorsoventrally (Fig. 10.6). Colored pigmentation develops soon after melanophores are fully recruited, resulting in dorsal and lateral coloration characteristic of the yellow phase (typically brownish-green or yellow-green), which is retained until metamorphosis to the silver phase. Ventral surfaces of yellow-phase anguillid Eels are generally lighter or more yellow in coloration than lateral or dorsal surfaces. The darkness or color cast of pigmentation in individuals can vary widely and is strongly influenced by lighting and the surrounding environment. Scales develop relatively late at 143–345 mm TL (Able & Fahay 2010).

Anguillid Eels retain this classic anguilliform fish body plan, an elongate, snakelike body, throughout the juvenile and adult life stages. Dorsal, caudal, and anal fins are conjoined into a continuous median fin around the posterior half of the body with rounded posterior margins. Pelvic fins are absent. Pectoral fins are relatively close to the head and generally rounded or somewhat pointed in the metamorphically advanced silver phase (Durif et al. 2000). All fins are soft rayed, and anguillid Eels have no spines or other hard external bony structures. The mouth of the post-leptocephalus phase is modest in size and terminal or slightly superior; teeth are setiform, small, and present on the maxilla, dentary, and ethovomerine bloc. Scales are cycloid, small, elongate, and deeply embedded below the epidermis. The opercular opening is a small, fleshy vertical slit. Eyes are small in the elver and yellow phases but become enlarged in the silver phase. Other body features are nondescript; color and patterning are relatively uniform with ventral surfaces lighter in color than lateral and dorsal surfaces, although skin pigmentation can be altered by varying illumination over short time periods (Eales 1968). These general features are relatively uniform for most species of *Anguilla*, although some subtropical species exhibit mottling of dorsal and lateral body surfaces.

Sexual Dimorphism

In general, the sexes of anguillid Eels are externally indistinguishable. Even so, females tend to grow larger than males, such that older *Anguilla* may have some size dimorphism between males and females. Just before sexual maturity (at the freshwater silver phase, before the spawning migration to the Sargasso Sea) the sexes at northern latitudes may be dimorphic with males being smaller (about 23–40 cm TL) than females (about 40–116 cm TL), although high regional variability occurs in absolute sizes of males and females (Able & Fahay 2010; Jessop 2010), and some overlap in size distribution of mature males and females usually exists. No other known external morphological features distinguish males from females in the freshwater yellow or silver phases.

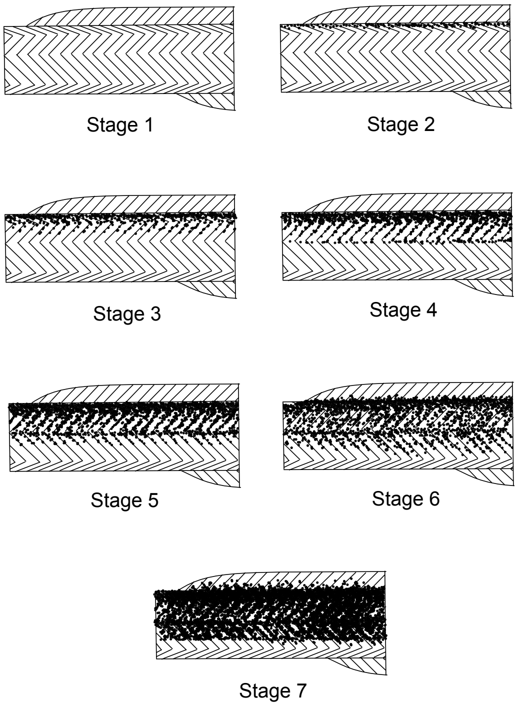

Figure 10.6. Development of lateral pigmentation (melanophores) in the glass-eel phase of the American Eel, *Anguilla rostrata* (simplified classification based on Strubberg's 1913 pigmentation classification for the European Eel, *A. anguilla*) (redrawn from Haro & Krueger 1988).

Transition to Silver Phase

Morphological transition to the silver phase is thought to adapt anguillid Eels to a pelagic migratory environment and generally results in darkening of the dorsal surfaces and pectoral fins to dark gray to jet black, while lateral surfaces become silvery or bronze as a result of recruitment of guanine crystals (Facey & Van den Avyle 1987; Fig. 10.7). The ventral surfaces in silver-phase anguillid Eels usually become white, although the anal pores can develop a black margin. The eye may enlarge to twice the diameter of the yellow phase, and retinal pigments become more sensitive to blue wavelength (Beatty 1975). Olfactory organs also enlarge, and pores of the lateralis system

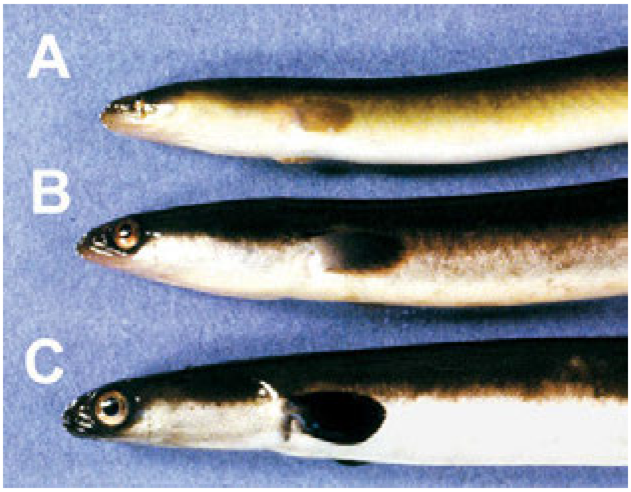

Figure 10.7. Morphology of (A) yellow-phase, (B) freshwater silver-phase, and (C) seawater-adapted and artificially matured male silver-phase American Eels, *Anguilla rostrata* (presumably as would appear during the spawning migration or at the spawning area). Note shift from yellow to black-silver coloration, blackening of pectoral fins, and enlargement of eye diameter.

become ringed with black pigment and more distinct. Other migratory, pre-spawning adaptations include cessation of feeding, degeneration of the gut (Gray & Andrews 1971; Pankhurst & Sorensen 1984), increase in fat content and red muscle mass, and increase in muscle performance (Ellerby et al. 2001). Oocyte diameter (Dutil et al. 1985) and gonad somatic index (gonad mass to body mass; McGrath et al. 2003) increase in the silver phase. Before spawning American Eels convert a considerable proportion of body mass to gonad development (Oliveira & Hable 2010).

GENETICS

Karyology

American Eels possess 38 diploid pairs of chromosomes, although characterizations of chromosome morphological categories vary between studies (e.g., 14 metacentric, 6 sub-telocentric, and 18 acrocentric pairs, Ohno et al. 1973, versus 11 meta- or sub-metacentric and 8 acrocentric pairs, Sola et al. 1981). Chromosome pair distribution is uniform in the various morphological categories. There is no evidence of morphologically differentiated sex chromosomes, and chromosome number and morphology are highly homogeneous in *Anguilla*, making karyology of limited value in ascertaining the evolutionary history of species in this genus (Sola et al. 1980).

Intraspecific Genetic Variation

The American Eel, similar to other anguillid Eels, is generally regarded as a single panmictic population of small effective size that lacks appreciable phylogenetic population structure (Avise 2003). American Eels exhibit no salient population divergence as evidenced by early mtDNA analyses throughout the Atlantic seaboard and Gulf of Mexico (Avise et al. 1986). More extensive molecular genetic analyses, however, show clinal variations in genetic structure, which imply that mating is not entirely panmictic and that dispersal of larvae is not entirely random with respect to location of continental residence of their parents (Avise 2003).

Genetic relationships and origins of American Eels and European Eels are unclear. The speciation event that resulted in the two distinct species is hypothesized to be the result of displacement of migrational circuits that led to a partial separation of the spawning areas, possibly as recently as the Pleistocene (2.6–0.01 mya) (Avise 2003). American Eels may hybridize with European Eels (presumably at the spawning area in the Sargasso Sea) to a minor degree (Avise et al. 1990) because hybrids occur in areas of geographic overlap (e.g., Iceland). An overall hybrid proportion of 15.5% occurs in Iceland, but ranges from 6.7% to 100% depending on life stages and locations, likely due to differential survival of hybrids and variation in hybridization rate through time (Albert et al. 2006).

PHYSIOLOGY

Leptocephalus Larvae

Little work has been conducted on the physiology of anguillid leptocephali due to difficulty in collection and their fragility. Metabolic assays have determined that leptocephali have some of the lowest rates of metabolism compared with body mass of any fish larvae, primarily because most of their body mass is composed of a nonmetabolic transparent energy storage material consisting primarily of glycosaminoglycan compounds, rather than muscle tissue (Bishop et al. 2000). Unlike other fish larvae, leptocephali devote most of their metabolism to respiration, rather than growth (Bishop & Torres 2001), which is logical given their long larval stage and relatively slow growth rates. Early-stage leptocephali possess no gills throughout the protracted larval stage, and respiration and salt secretion during this long marine phase occurs across the body surface.

These functions are transferred to the gills as they develop in the later-stage leptocephalus, glass-Eel, and adult stages (Kaneko et al. 2003).

Post-larval Respiration

The generalist lifestyle of post-larval anguillid Eels dictates a physiology that accommodates a variety of environments, often to an extreme degree or with rapid transition from one environment to another. Respiration via the gills is modest in comparison to that of other teleosts, and oxygen consumption is relatively low; however, considerable gas exchange occurs across the skin. Most aerobic activity is limited as reflected in relatively slow swimming and long periods of inactivity associated with a benthic lifestyle, although adult migrant anguillid Eels can maintain aerobic, low-speed swimming for long periods in fresh and salt water. Anguillid Eels can also maintain respiration out of water for long periods; typically the branchial chamber is filled with air with some absorption of oxygen via the gills, but the majority of gas exchange occurs cutaneously. Anguillid Eels are not particularly well-adapted for gas exchange in air but have an unusual tolerance to hypoxemia (Hyde et al. 1987) and are highly tolerant of water with low dissolved oxygen levels (McKenzie et al. 2003).

Salinity Tolerance

Glass Eel, elver, yellow-phase, and silver-phase anguillid Eels are typically euryhaline to some degree, and exhibit an ability to move between freshwater and saltwater environments regularly with minimal osmoregulatory or other physiological stress. Nevertheless, some acclimation to waters of differing salinity appears to be required. Transformation to the migratory silver phase in fresh water is accompanied by several physiological pre-adaptations to the subsequent migration in the marine environment, including increase in gill chloride cell number and Na^+, K^+-ATPase activity (Fontaine et al. 1995; Kaneko et al. 2003). Other pre-adaptations include lengthening of the rete mirabile and increase in swim bladder wall guanine content, presumably to maintain gas secretion into the swim bladder at increased migratory depths (Kleckner & Krueger 1981).

Thermal Tolerance

Anguillid Eels are highly tolerant of a wide range of water temperatures; normal activity usually occurs over a range of 10–23°C. American Eels cease feeding, show reduced activity, and become torpid (metabolically depressed) at water temperatures <10°C (Walsh et al. 1983), although glass Eels may appear in estuaries in January at a water temperature of −0.8°C (Jeffries 1960). Final preferred temperature of yellow- and silver-phase American Eels in fresh water is between 17 and 20°C (Barila & Stauffer 1980; Karlsson et al. 1984; Haro 1991) and is not significantly different between fresh and salt water, yellow or silver phases, or maturation states (Haro 1991). The upper lethal temperature is not known for the American Eel but is likely <30°C. Anguillid Eels in thermally stratified water bodies (lakes and the open ocean) may regularly cross the thermocline.

Vision

Anguillid Eels have color vision, and possess both rods and cones in the retina (Pankhurst 1984), with rods predominating as they metamorphose to the silver phase. Yellow-phase American Eel have retinal pigments with mixtures of rhodopsin $P501_1$ and porphyropsin $P523_2$, but silver-phase downstream migrants have mixtures of rhodopsins $P482_1$ and $P501_1$, with reduced amounts of porphyropsin $P523_2$, the latter in only small amounts (Beatty 1975). Sexually matured and seawater-adapted silver-phase American Eels have only the two rhodopsins with $P482_1$ predominating. The changes in retinal pigment proportion with maturation may reflect increased sensitivity to blue wavelengths and visual adaptation to the pelagic ocean environment.

Olfaction

Anguillid Eels have exceedingly sensitive olfactory capability, being able to discern odors at concentrations of $<1:10^{18}$ parts, exceeding that of most fishes and probably most other vertebrates (Tesch 2003). Salinity and temperature may also be more important than odor in determining orientation of anguillid glass Eels (Tosi et al. 1990), and olfaction interacts strongly with rheotaxis in anguillid Eel foraging behavior (Carton & Montgomery 2003) and glass Eel and elver migration in fresh water (Sorensen 2009). Organic odorants were identified as chemoattractants in anguillid Eels (Tosi & Sola 1993; Sola 1995), possibly a product of microbial decomposition of detritus (Sorensen 1986). Other identified attractants include bile salts (Sola & Tosi 1993), amino acids (Sola & Tongiorgi 1998), and skin mucus of conspecifics (Saglio 1982). Anguillid Eels are particularly adept at recognizing and being attracted to general water-borne odors from conspecifics (Briand et al. 2002; Sorensen 1986). Attraction by conspecific or pheromone odors may function to assist in location of mates at sea during spawning, but probably only at relatively short distances, given extreme dilution at an oceanic scale (Sorensen 1986).

BEHAVIOR

Leptocephalus Larvae

Anguilla leptocephali in the open ocean are solitary, nonschooling, and thought to generally drift passively with oceanic currents within the upper several hundred meters of the water column. Even so, leptocephali may undertake regular vertical diel migrations within this zone. Larvae between 5 and 10 mm TL occur between 100 and 150 m during the day and between 50 and 100 m at night (Castonguay & McCleave 1987) presumably to feed. Leptocephali may undertake active swimming during the oceanic phase, although it is not known if swimming is navigational or directed toward a migratory goal. The larval stage can react and actively swim to avoid predators or other threats (Miller 2009).

Glass Eels and Elvers

Upon reaching the continental shelf, American Eel leptocephali metamorphose to the glass-Eel phase and forgo a pelagic existence to a largely benthic one. Glass Eels in coastal zones and entering tidal reaches of estuaries, however, frequently exhibit selective tidal stream transport. This enables them to drift passively landward while suspended in the water column during flood tides but to descend and hold position on or near the bottom during ebb tides (Wippelhauser & McCleave 1987). This behavior presumably facilitates movements toward freshwater habitats while minimizing energy expenditures of swimming against outgoing tides. Glass Eels appear to use olfaction to identify and locate fresh water (Sorensen 1986; Sorensen & Bianchini 1986). Entry into fresh water appears to be mediated by temperature. American Eels may arrive at estuaries in northern latitudes in midwinter at subzero water temperatures (Jeffries 1960) but do not usually ascend into fresh water until water temperatures are >10°C (Haro & Krueger 1991; Jessop 2003). Upstream movements of elvers in fresh water at northern latitudes peak at 11–16°C early in the migratory season; temperature appears to have less influence on upstream migration later in the season (Jessop 2003). Migration of glass Eels and elvers can also be influenced by river flows and tidal cycles (Sorensen & Bianchini 1986; Wippelhauser & McCleave 1987; Jessop 2003). Thus, large numbers of glass Eels are usually observed at the salt and fresh water interface in the spring months. Arrival of glass Eels in fresh water and upstream migration of elvers usually occurs earlier at more southern latitudes (Vladykov 1966), but local exceptions to this trend occur (Facey & Van den Avyle 1987; Jessop 2000). Glass Eels and elvers that reach flowing fresh water may seek lower water velocities in the boundary layer at river margins or near the bottom or through interstitial spaces of open substrates (Sheldon & McCleave 1985; Barbin & Krueger 1994) to maximize upstream progress and minimize energy expenditure. Velocity barriers or areas of water flow over high slopes may be overcome by climbing on wetted surfaces of flow margins at least for small anguillid Eels. Individuals may ascend physical barriers of this type over hundreds of meters (Sheldon 1974). Upstream movements of American Eels are largely nocturnal (Dutil et al. 1989) and continue during warmer months for the first several years of freshwater life (Haro & Krueger 1991). Large concentrations of upstream migrant American Eels may occur at dams or other barriers that inhibit or delay upstream ascent. Densities of American Eels generally decrease with distance upstream, but densities are not strongly or consistently related to habitat features (e.g., habitat type, abundance of cover, water temperature, or density of predators; Smogor et al. 1995). Freshwater movements, climbing behavior, and general activity tend to be nocturnal.

Movement, Homing, and Home Range

After several years in fresh water, American Eels usually cease upstream migration, become sedentary, and tend to establish a home range. Behavior throughout most of the rest of their lives reflects that of a solitary, territorial, nocturnal benthic predator. Movements within the home range generally occur as foraging bouts at night with remarkable regular homing back to a specific daytime refuge. Displaced American Eels also appear to home back to their home range with considerable accuracy over displacement distances of several kilometers (Parker 1995) to ≤80 km (Vladykov 1971). In rivers and streams, home range of American Eels is typically <10 river km (Oliveira 1997; 1999; Morrison et al. 2003), but in lakes home range varies from 3 to 65 ha (LaBar & Facey 1983; Thomas 2006). In estuarine environments home ranges appear to be generally more restricted than in fresh water and can vary in size from <60 m (Gunning & Shoop 1962) to several hectares (Helfman et al. 1983; 1987; Bozeman et al. 1985; Ford & Mercer 1986; Dutil et al. 1988; Morrison et al. 2003), although ranges in tidal estuaries can be ≤325 ha (Parker 1995).

Large-scale movements may be undertaken seasonally. American Eels may move during the autumn months from summer feeding areas to overwintering areas less prone to winter temperatures ≤0°C (i.e., from estuaries to freshwater habitats), then return to summer habitats in the spring (Morrison et al. 2003; Lamson et al. 2006; Thibault et al. 2007). Overwintering behaviors may also include burrowing into soft sediments for extended periods of time (Chaput et al. 1977), often in aggregations of tens to hundreds of individuals.

During the yellow phase, anguillid Eels with established territories may become aggressive toward other conspecifics and often are cannibalistic with respect to smaller individuals entering their territory. Yellow-phase anguillid Eels often seek daytime shelters within aquatic vegetation, under rocks or logs, or within other available cavities. Large cavities in areas of limited shelter availability may often be occupied by several individuals of similar size. Juveniles and adults remain cryptic during the day and may retreat into cavities or shelter in the presence of larger predators, emerging to forage primarily at night, although they may actively forage during the day, especially in tidal areas (see ecology section).

Swimming

Locomotion in anguillid Eels is primarily via anguilliform swimming; as such they are regarded as relatively weak swimmers but can swim at surprisingly high sprint speeds for short periods of time (McCleave 1980). Glass Eels and elvers of anguillid Eels may swim actively in flowing water, but elvers may refuse to swim against water velocities >25 cm/s (Jessop 2000; 2003), and migration of glass Eels and elvers can be delayed by high velocities (Jessop & Harvie 2003). Critical swimming speeds (U_{crit}) in anguillid Eels are 0.97 body length/s for the yellow phase and 1.2 to 1.7 body lengths/s for the silver phase (Quintella et al. 2010). Conversely, anguillid Eels may swim at slower sustained speeds for long durations and distances, presumably for several months and thousands of kilometers during the spawning migration (van den Thillart et al. 2004). Anguillid Eels are also adept at burrowing into many types of substrates and can swim backward. Their body is highly flexible and can bend >360 degrees. They can also leap from water at least 1 body length, are adept at climbing, and may travel out of water for considerable distances. At small sizes, anguillid Eels can adhere to wetted substrates by surface tension and can crawl vertically up rough wetted surfaces for many meters (Solomon & Beach 2004), which aids in exploitation of freshwater habitats inaccessible to other fishes. Climbing behavior of anguillid Eels typically occurs at night and at significantly higher water temperatures than active upstream swimming behaviors (White & Knights 1997; Linton et al. 2007). Locomotory modes in water and on land are significantly different in American Eels. While swimming in water, the amplitude of lateral undulations is about 0.08 times body length with little change in amplitude at the head and a temporal lag between maximal flexion and body displacement. During locomotion over land, lateral undulations are more uniform over the entire body length with no lag between flexion and displacement (Gillis 1998).

REPRODUCTION

Sexual Differentiation

American Eels are morphologically sexually indeterminate until reaching about 300 mm TL (Krueger & Oliveira 1997); at that point gonads begin to differentiate into testes or ovaries (but full sexual maturation may not occur until many years thereafter).The mechanisms of sexual differentiation of anguillid Eels into male or female are unclear; environment, competition, and growth rate are suspected to play major roles (Colombo & Grandi 1996; Krueger & Oliveira 1999; Oliveira et al. 2001). Sex ratios of anguillid Eels in most locales are rarely equal and usually highly skewed, but the actual mechanisms of environmental sex determination are unclear. High population densities are thought to promote a higher proportion of males in a population, which is supported by observed increased production of males in high-density aquaculture conditions (Colombo & Rossi 1978; Egusa 1979).The proportion of female American Eels in local populations was thought to generally increase at higher latitudes or distance inland (Vladykov 1966). Additional studies showed local exceptions to these trends (Winn et al. 1975; Oliveira & McCleave 2000), and the mechanism of sex determination in fresh water appears to act at the river or habitat level. Lacustrine environments tend to favor production of females, and coastal riverine environments or areas of high American Eel density tend to favor production of males

(Oliveira et al. 2001). It is unknown whether there are differences between males and females in upstream migratory behavior or habitat selection. Both sexes can usually be found in all types of habitats but frequently in different proportions.

Spawning Migration to the Sea

Upon reaching a particular size or age, American Eels metamorphose to the silver phase, cease feeding, abandon their home range, and begin a downstream spawning migration to the ocean. American Eels may begin their migration back to the Sargasso Sea at a variety of ages with males tending to emigrate at significantly younger ages than females (Gray & Andrews 1971; Harrell & Loyocano 1982; Oliveira 1999). Age alone, however, is not a reliable predictor of time of emigration (Oliveira 1999). This variability in age at emigration, coupled with trends in lower growth rates of males and higher growth rates of females, supports the hypothesis that males use a time-minimizing strategy in emigration (i.e., emigrating at the minimum size required for successful migration to the Sargasso Sea), and females use a size-maximizing strategy (e.g., emigrating at older ages and larger sizes to maximize egg production before spawning) (Helfman et al. 1987). Confirmation of this hypothesis with field data suggests that females may actually adopt a tradeoff between the two strategies that is dependent on environment-specific growth rate (Oliveira 1999; Oliveira et al. 2001).

Initiation of downstream migration in temperate silver-phase anguillid Eels typically occurs during the autumn months (Haro 2003). Peaks of movement usually correspond to high-flow events but are relatively unpredictable within a season (Vøllestad et al. 1986). Latitudinal variation in timing of emigration occurs in the American Eel with peaks of emigration occurring in northern Canada as early as July and in Florida as late as January (Haro 2003). Years with few high-flow events may result in smaller run sizes. Downstream movement usually starts at nightfall but is reduced during the early morning hours; few downstream migrants move during the day (except at high flow or turbidity), when they seek shelter and suspend migration until the following nightfall (AH unpubl. data). Downstream migration rates can be rapid with individuals moving at rates ≤50 km/day. Upon reaching tidal areas, silver-phase American Eels may adopt a selective tidal stream transport behavior to maximize seaward migration rate, actively swimming in the water column during ebb tide but maintaining position on the bottom during flood tide (Parker & McCleave 1997; Barbin et al. 1998). Olfaction may play a role in mediating downstream migration and transition to the marine environment (Barbin et al. 1998). Anguillid Eels move relatively quickly from fresh water to salt water with little or no physiological acclimation delay.

Spawning migration within coastal and open ocean environments is poorly understood in anguillid Eels. No individual American Eel has been tracked to the Sargasso Sea, and captures or observations of migrants at sea are few (Wenner 1973; Robins et al.1979). Ocean migration may be active and directed to the spawning area (McCleave & Kleckner 1985), but the depths and routes of migration, as well as potential schooling behaviors, are unknown. Morphology and physiology of metamorphically advanced individuals suggest they are adapted to migrate within the upper 1,000 m of the ocean within the photic zone (Kleckner & Krueger 1981; but see Robins et al. 1979). Migrant anguillid Eels in the open ocean may also undertake regular diel vertical migrations of several hundred meters that may function in predator avoidance (Tesch & Rohlf 2003; Jellyman & Tsukamoto 2005). The migration of American Eels to the Sargasso Sea presumably takes 2–8 months to complete with spawning occurring between February and April, and possibly later, based on energetic reserves and timing of appearance of eggs and larvae in the Sargasso Sea (McCleave et al. 1987).

Spawning Area

Migrant anguillid Eels may use thermal or chemical cues associated with strong surface thermal fronts formed between the northern and southern Sargasso Sea water masses to initially identify the general spawning area and cease migration (Kleckner at al. 1983; Kleckner & McCleave 1985, 1988). Adult American Eels have never been observed in the Sargasso Sea, but spawning of both American Eels and European Eels is presumed to occur on the warm side of a regularly formed subtropical thermal and salinity convergence front in the vicinity of 52 degrees W to 79 degrees W longitude and 19.5 degrees N to 29 degrees N latitude (McCleave et al. 1987). Because the smallest larval American Eels (<5 mm long, presumably ≥9 days old, based on growth rates of laboratory-reared larvae, Oliveira & Hable 2010) only occur at depths of 50–350 m, spawning is assumed to occur near or within this depth range (Kleckner & McCleave 1982) or at least within the upper 1,000 m.

Fecundity

Fecundity of American Eels in Chesapeake Bay is estimated from 400,000 (about 500 mm TL) to 2.5 million (about 850 mm TL) eggs/silver-phase female (Wenner & Musick 1974), but estimates are considerably higher for silver-Eel females in Maine and Canada that range to >20 million for females approaching 1,000 mm TL (Barbin & McCleave 1997; Tremblay 2009; Table 10.1). Causes for the geographic difference in fecundity are unclear, and more comprehensive sampling is needed to more accurately estimate fecundity for the entire American Eel population.

Spawning Mode

American Eels are probably pelagic broadcast spawners; it is unknown whether fertilization of eggs occurs in single or multiple events. Spawning likely occurs sporadically over a relatively large geographic area. Adults presumably die soon after spawning, given their enormous investment in gamete production and expenditure of energy and body mass during the course of migration (Oliveira & Hable 2010; Fig. 10.8). The mechanism of location of mates and spawning behaviors are unknown. Laboratory observations suggest that male American Eels may use olfaction to locate females via pheromones issued from ovulating females (Sorensen & Winn 1984; Fig. 10.8).

Eggs, Embryos, and Larvae

Development of eggs, embryos, and early larvae in *A. rostrata* is described solely from artificial maturation and fertilization experiments in the laboratory at water temperatures of 20°C (Oliveira & Hable 2010). Oocytes at the time of natural spawning range from 960–1030 um in diameter with multiple oil droplets and a distinct cortical nucleus. Embryogenesis is rapid with early somite-stage embryos formed about 20 h after fertilization and hatching occurring after about 50 h after fertilization. Larval size at hatching is 2.7±0.2 mm TL with growth to 3.8±0.3 mm TL 4 days after hatching (at a mean rate of 0.28 mm/day), and near-complete absorption of the yolk sac 6 days after hatching (Oliveira & Hable 2010; Fig. 10.9).

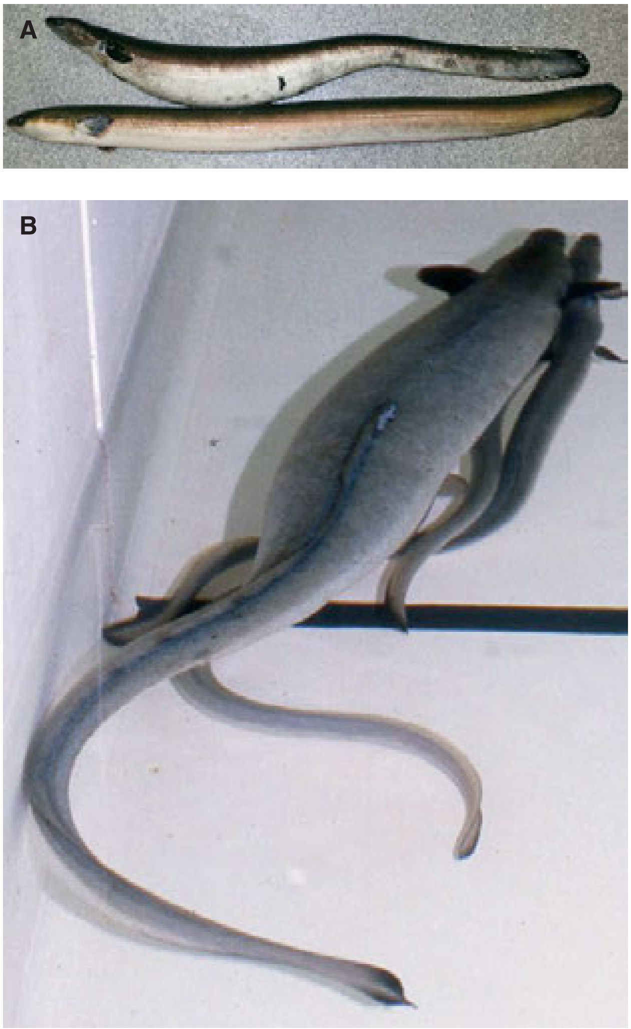

Figure 10.8. (A) Upper fish is artificially matured female American Eel, *Anguilla rostrata*, showing extreme gonadal growth; lower fish is unmatured freshwater downstream migrant female (photograph courtesy of and used with permission of K. Oliveira, University of Massachusetts). (B) Artificially matured male and female American Eels, allowed to interact naturally in a laboratory tank. Note "consort" of three smaller males maintaining body contact with single larger female (photograph courtesy of and used with permission of P. Sorensen, University of Minnesota).

ECOLOGY

Habitat

The post-larval American Eel occurs in perhaps the broadest diversity of habitats of any fish species, including oligotrophic to eutrophic freshwater habitats, estuaries, and coastal marine habitats as far offshore as the outer continental shelf. These habitats include clear, small, unproductive headwater streams; large, turbid, productive mainstem

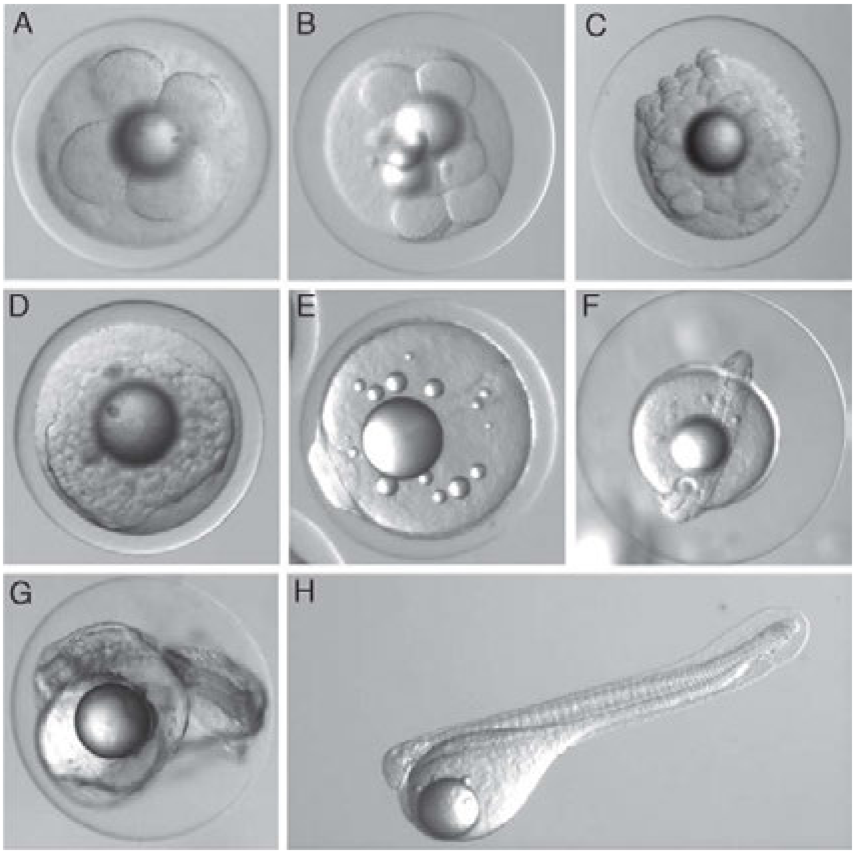

Figure 10.9. Developing ova and newly hatched, laboratory-reared larva of the American Eel, *Anguilla rostrata* (from Oliveira & Hable 2010 and used with permission of K. Oliveira, University of Massachusetts).

rivers; blackwater swamps and rivers; subterranean springs and caves; clear and turbid, deep and shallow, vegetated and barren lakes and ponds; and fresh, brackish, and salt water marshes (Helfman et al. 1987; Table 10.1). In more northerly habitats, the American Eel may be the dominant fish species, both numerically and in biomass (Smith & Saunders 1955; Ogden 1970; Jacobs et al. 2003). Anguillid Eels are classified as ecological generalists, considered an advantageous strategy given that leptocephali may ultimately be distributed to a great variety of potential habitats by ocean currents (see introductory section; Fig. 10.1). Anguillid Eels do not appear to be bound to any particular habitat throughout their lives; after many years in freshwater individuals may transition to estuarine or marine environments (where they may remain for the rest of their lives) or vice versa (Jessop et al. 2006; Lamson et al. 2006). Regular seasonal movements between estuarine and freshwater habitats may also occur (Secor 1999; Morrison et al. 2003).

Juvenile and adult American Eels are primarily benthic, and preferentially seek habitat offering hiding places during the day including beneath rocks, boulders, or woody debris; within dense aquatic vegetation; or in loose detritus, mud, or sand (Vladykov 1955; Fahay 1978; Ford & Mercer 1986; Goodwin & Angermeier 2003). Anguillid Eels are proficient burrowers and can quickly conceal their entire body in loose benthic substrate. At night they emerge to forage primarily near the bottom but can occur in midwater to forage on pelagic food sources. American Eels may occur at a variety of depths in freshwater and estuarine habitats but tend to spend most of their time at shallow depths between 1 and 5 m (Facey & LaBar 1981, 1983; Thomas 2006). The maximum depth of occurrence in marine environments is unknown, but anguillid Eels have been observed at ocean depths of ≤2,000 m (Robins et al. 1979).

Larval Diet

Food and feeding of larval anguillid Eels are little studied. Early researchers speculated (incorrectly) that leptocephalus larvae did not feed but absorbed dissolved organic carbon across the body surface (Pfeiler 1986). Additional work identified active feeding and a functional gut in leptocephali of anguillids (Mochioka et al. 1993) and specifically *A. japonica* (Tanaka et al. 2001), but identification of specific prey items in the larval diet remains problematic. Identified prey in other anguillid leptocephali include fecal pellets of zooplankton (or possibly bacteria growing on similar pelagic particulate material), ciliates, and larvacean houses (Miller 2009). Specific prey of larval American Eels may be similar but as yet are unknown.

Post-larval Diet

Post-larval American Eels are carnivorous, feeding primarily on a variety of live food sources. Glass Eels have little identifiable gut contents, but elvers may feed primarily on chironomid and simuliid (Diptera) larvae (Dutil et al. 1989). Yellow-phase American Eels characteristically show an increased prey size with an increase in body size. In fresh water, yellow-phase American Eels <40 cm TL prey primarily on larval stages of Ephemeroptera, Megaloptera, and Trichoptera, and individuals >40 cm TL feed more frequently on fishes with benthic or prey fishes that are poor swimmers more common in stomach contents (Ogden 1970). The transition to increased piscivory, however, may occur in American Eels as small as 250 mm (Lookabaugh & Angermeier 1992). The prey of American Eels >60 cm TL can be almost exclusively fishes and crayfishes (Ogden 1970). Proportion of prey items in stomach contents tends to reflect proportion of available benthic prey. Other diet items of American Eels (>10 cm TL) include larval odonates and chironomids, oligochaetes, polychaetes, gastropods, mysid shrimps, isopods, amphipods, crabs, astacids, and decapod crayfishes (Able & Fahay 2010). Diets in marine and estuarine habitats also include small crustaceans and mollusks (Smith & Saunders 1955; Godfrey 1957). Additional minor food items include detritus and carrion, primarily dead fishes, but fish eggs may be consumed by American Eels (Knotek & Orth 1998); in particular juvenile and adult American Eels feed in quantity on eggs of several species of anadromous *Alosa* during the spring (Clupeidae, Herrings; Able & Fahay 2010). Large American Eels may be cannibalisitic on small individuals (Jessop 2000). Due to their long period of occupation of freshwater habitats and ultimate emigration from fresh water as large adults, anguillid Eels likely contribute to a net transport of nutrients out of freshwater systems (Smith & Saunders 1955).

Foraging may be largely via olfaction, although anguillid Eels can probably visually perceive prey to some degree. Anguillid Eels typically explore benthic habitat for prey, and their flexible body form allows them to search cavities, holes, and burrows for food. They will also scavenge carcasses and can tear chunks of flesh or organs from carcasses via rotational feeding (i.e., biting and holding the carcass while spinning their body in order to pull against the carcass with additional tearing force) (Helfman & Clark 1986).

Predators

A variety of animals prey on American Eels at all life stages. Anguillid leptocephali are likely consumed by larger marine planktivores, but direct observations have not been made and the fragile and gelatinous nature of leptocephali makes them difficult to identify in stomach contents (Miller 2009). In estuaries and fresh water, glass Eels and elvers are heavily preyed on by fishes, herons, aquatic mammals, and even terrestrial passerine birds. Watersnakes (*Nerodia* spp.; Figure 10.10), osprey, and other large piscivorous birds frequently feed on yellow-phase American Eels. In estuaries and marine environments, large yellow-phase and migrant silver-phase American Eels are common prey for large fishes such as Haddock (*Melanogrammus aeglefinus*), Striped Bass (*Morone saxatilis*), Bluefish (*Pomatomus saltatrix*), and occasionally Sharks and Swordfish

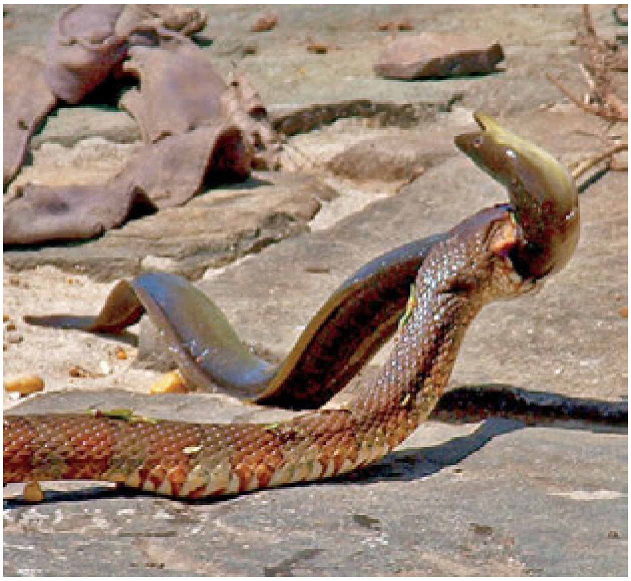

Figure 10.10. An American Eel, *Anguilla rostrata*, caught in the jaws of a Northern Watersnake (*Nerodia sipedon sipedon*). After some reorientation, the Northern Watersnake swallowed the American Eel (Delaware and Raritan Canal State Park, Raritan River drainage, Somerset, New Jersey, 7 April 2010; photograph by and used with permission of Bill Bonner).

(*Xiphias gladius*) (Scott & Crossman 1973; Ernst & Ernst 2003; Able & Fahay 2010).

Parasitism

American Eels are a host to a wide variety of freshwater fish parasites including at least 8 protozoans, 1 monogenean, 21 trematodes, 7 cestodes, 16 nematodes, 21 acanthocephalans, and 7 crustaceans (Hoffman 1999). The following parasites are also specific to American Eels: *Gyrodactylus anguillae*, *Pseudodactylogyrus anguillae*, *Bothriocephalus claviceps*, *Proteocephalus macrocephalus*, *Daniconema anguillae*, *Paraquimperia tenerrima*; *Paraquimperia aditum*, *Ergasilus celestas*, and *Crepidostomum brevivitellum* (Marcogliese & Cone 1993).

American Eels have recently become a host of the exotic Asian swim bladder nematode parasite, *Anguillicoloides crassus*. The parasite has spread northward from an initial invasion point in Texas (Johnson et al. 1995) and now infects American Eels northward to the Canadian Maritimes (Barse & Secor 1999; Aieta & Oliveira 2009) with a possible future expansion northward to the Gulf of St. Lawrence. Juvenile American Eels acquire the parasite by ingestion of an infected copepod or other intermediate paratenic host; developing nematodes exit the gut and migrate to the swim bladder lumen. Adult nematodes feed on the host's blood supply and may compromise swim bladder function, which may ultimately affect oceanic migration success in adult American Eels (Sures & Knopf 2004).

American Eels also may function as a host to glochidia of several freshwater mussel species. The glochidia of the following mussel species infest American Eels in the wild, but transformation of the glochidia into adults was not documented: *Actinionaias ligamentina*, *Megalonaias nervosa*, and *Arcidens confragosus* (Surber 1915; Wilson 1916; Coker et al. 1921). The federally endangered *Elliptio complanata* also use American Eels as primary hosts (Lellis 2002), and transformation of this species on American Eel has been documented in the laboratory (Minkkinen et al. 2010).

CONSERVATION

In North America, conservation of American Eels has received little attention until recently. Observations of decline of recruitment of American Eels were initially noted in the early 1990s (Castonguay et al. 1994); before this period little quantitative monitoring of populations occurred, and few comprehensive management plans for American Eels existed. Subsequent informal analyses of population trends coastwide indicated stable or declining trends (Haro et al. 2000), although the data were sparse and unstandardized. Intense glass Eel harvest in the 1990s, coupled with indications of significant local population declines, prompted agencies to seriously review the population status of American Eels. More recent data indicated significant declines of American Eels throughout their range, although declines were apparently more severe in some locations (e.g., St. Lawrence River, Lake Ontario) than others (Fig. 10.11). Cause of the population decline is unknown although anthropogenic factors (e.g., habitat loss, barriers to migration, harvest, and pollution) may be significant. Contamination of older Eels by bioaccumulated polychlorobiphenyls (PCBs) may reduce viability of silver-phase American Eels and their ability to swim to the spawning area in the Sargasso Sea (Robinet & Feunteun 2002). Non-anthropogenic factors, possibly related to ocean conditions, may also be at play. A significant negative correlation occurs between the North Atlantic Oscillation and trends in catches of glass-Eel stages of the European Eel, lagged by 1 year. Ocean-atmospheric changes in the Sargasso Sea may also affect the ability of adults to locate the spawning areas and possibly the survival of leptocephali (Friedland et al. 2007), which presumably would similarly affect migration and survival of the American Eel.

In Canada, the American Eel is listed as a Species of Special Concern nationally, and a National Management Plan has been drafted (Canadian Eel Working Group 2009). The American Eel is considered an endangered species in Ontario, and a Draft Recovery Strategy has been developed for the species in that province (MacGregor et al. 2010). In the United States, the American Eel was petitioned to be listed as an Endangered Species in 2009; but ultimately was not listed, and the species receives no federal protection or special federal status. Nonetheless the Atlantic States Marine Fisheries Commission (ASMFC) has developed a coastwide management plan for the American Eel (ASMFC 2000), and all member states (all coastal states from Maine to Florida) are seeking to comply with management goals of the ASMFC plan by modifying their own state management plans and adopting standardized monitoring protocols. A review of global status of the American Eel has classified the species as Apparently Secure for Canada and the United States; Critically Imperiled in Ontario and South Dakota; Imperiled in Illinois, Indiana, Kansas, Ohio, Vermont, West Virginia, and Wisconsin; Vulnerable in

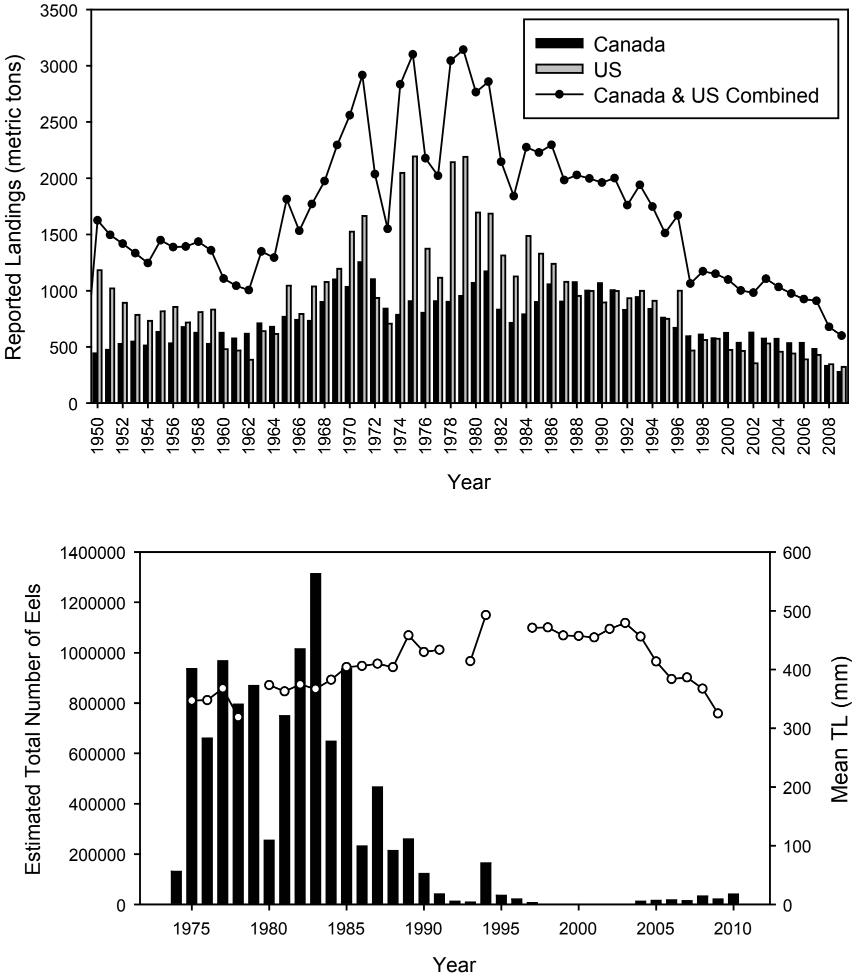

Figure 10.11. Top: Reported landings of American Eel, *Anguilla rostrata* (all life phases, but primarily yellow and silver phases), for Canada (black bars), the United States (gray bars), and North America (line), 1950–2009. Data courtesy of V. Tremblay (AECOM American Eel COSEWIC writer), D. K. Cairns, R. Bradford, G. Veinott (Department of Fisheries and Oceans, Canada), Yves Mailhot (Ministère des Ressources naturelles et de la Faune du Québec, Canada), and G. Nesslage (Atlantic States Marine Fisheries Commission). *Bottom*: Total number of American Eels ascending the eel ladders at the Moses-Saunders Dam (New York and Ontario; St. Lawrence River) for 1974–2010 (black bars) and associated changes in annual mean TL (line). Days of operation for the Moses-Saunders eel ladder varied greatly among years (33–154 days). Operation of a second ladder (the Moses ladder) began in 2006. Long-term decrease in numbers of American Eels ascending the ladders is indicative of reduced recruitment but note the slight increase in numbers from 2004 to 2010 associated with decrease in mean TL. Data courtesy V. Tremblay (AECOM American Eel COSEWIC writer), A. Mathers (Ontario Ministry of Natural Resources), and K. McGrath (New York Power Authority).

Quebec, Georgia, Iowa, Massachusetts, New Hampshire, New York, Oklahoma, and Tennessee; Apparently Secure in Labrador, Prince Edward Island, Arkansas, District of Columbia, Kentucky, Maryland, and North Carolina; and Presumed Extirpated in New Mexico (NatureServe 2010).

Most conservation and management plans identify several specific areas where conservation efforts for American Eels should be focused. These include more stringent limitations on commercial and recreational harvest, protection and enhancement of habitats, controls on potential contaminants and disease, and removal or mitigation of migratory barriers or threats (e.g., dams). Given reduction in available habitat by exclusion of upstream migrant American Eels by dams, and high mortality incurred by passage of downstream migrants through hydroelectric turbines, passage mitigation and development of appropriate passage technologies are high conservation priorities in most plans.

COMMERCIAL IMPORTANCE

American Eels have a long history as a human resource and were highly valued by Native North Americans and early European settlers for consumption and other practical uses (Casselman 2003; MacGregor et al. 2009). American Eels continue to rank highly in terms of cultural, spiritual, and ceremonial significance for Native Americans as well as a food source and are considered indicators of habitat integrity (COSEWIC 2012). Among freshwater fishes, American Eels have high energy value / unit weight, are easily preserved for long-term storage and transport, and generally fetch a higher price / unit weight than most other freshwater species. Historically American Eels were harvested for direct consumption, primarily in the yellow and silver phases, and were frequently smoked or dried for long-term storage. American Eels are also often harvested for bait for recreational fishing or as preferred bait for the commercial blue crab pot fishery in Chesapeake Bay. American Eels are most frequently collected by spearing, netting, and trapping. Techniques often target downstream migrant American Eels in autumn with purpose-built nets or weirs, occasionally for live export to Europe or elsewhere. Prices for yellow- and silver-phase American Eels vary widely both annually and regionally but generally range between US$0.50 and $1.00/kg (ASMFC 2000). Yellow-phase American Eels used for recreational bait can fetch >US$2.00/individual. More recently, a specialized fishery for American Eel glass Eels and elvers has developed for live export to the aquaculture industry in Europe and Asia with prices for live individuals reaching ≤US$900/kg. Recent development of more comprehensive management plans for American Eels in the United States and Canada have enabled tighter control on catch and trade for both commercial and recreational fisheries.

Few records were kept on American Eel catch and effort before the early 1900s (MacGregor et al. 2008), making historic commercial importance and recent trends relative to population levels before European settlement difficult to assess. Catch between the United States and Canada has been relatively equal since the early 1900s (Fig. 10.10) with a long-term mean catch of about 1,500 mt annually for both countries combined. Recent harvest has declined significantly and is currently <25% of the long-term mean (Casselman 2003). Regional catches may vary widely, but trends in catch are generally decreasing in most regions. Decreasing recruitment of glass Eels, elvers, and subsequent reduced abundance (Fig. 10.10) may be influencing harvest of American Eels of marketable size. Prognosis of both commercial and recreational fisheries for the future is dim, based on reduced recruitment, lower harvest, and decreased catch/unit effort; many traditional commercial fisheries for yellow- and silver-phase American Eels have collapsed or are economically inviable (Casselman 2003).

LITERATURE GUIDE

Several books have been written on general biology of anguillid Eels; none is more comprehensive and detailed than Tesch (2003 and previous editions), which, although focusing on the European Eel, draws from much comparative data for other species of *Anguilla*. Bertin (1956) and Moriarty (1978) provided similar reviews for the European Eel with additional cultural and commercial perspective; van Ginneken & Maes (2005) reviewed later findings concerning European Eel and American Eel oceanic and spawning biology. In an excellent work, Aoyama (2009) reviewed more current research on *Anguilla*, particularly with respect to evolution, biogeography, and oceanic life history, and Miller (2009) added particular detail to morphology, life history, and ecology for the infrequently studied leptocephalus stage. Later international symposia on anguillid Eels, particularly with reference to culture, conservation, and management can be found in Aida et al. (2003), Casselman & Cairns (2009), Dixon (2003), and Loftus (1982). Facey & Van den Avyle (1987) provide a basic species profile for the American Eel.

Additional technical aspects on American Eel stock status and management are reviewed in several management reports and plans, including Atlantic States Marine Fisheries Commission (ASMFC 2000 and subsequent addenda and Stock Assessment Reports), Department of Fisheries and Oceans Canada (2010), and Peterson (1997), Casselman (2003) and MacGregor et al. (2009) reviewed broader perspectives on American Eel conservation and management philosophy. Solomon & Beach (2004) provided a notably comprehensive review of technical aspects of upstream passage of *Anguilla*, and Electric Power Research Institute (2001) similarly reviewed downstream passage.

Acknowledgments

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Chapter 11 Engraulidae: Anchovies

Lisa J. Hopman and Carter R. Gilbert

The Engraulidae (Anchovies) is a member of the order Clupeiformes (Herrings), a taxonomically well-differentiated group of five families forming one of the more basal groups of teleostean fishes (Nelson 2006). The most distinctive morphological characters of Anchovies are their large mouths and rounded snouts. Anchovies are usually small, silvery, schooling fishes that generally feed on zooplankton (Jones et al. 1978), and some species have a unique system of detecting polarized light that may be used in feeding and schooling (Novales Flamarique & Hárosi 2002). Engraulidae comprises 16 genera and about 140 species (Nelson 2006; but see Bloom & Lovejoy 2012) that are found typically in warm inshore marine waters worldwide (Jones et al. 1978). Several species (about 18), however, migrate into rivers, and some live permanently in fresh water (Grande & Nelson 1985; Nelson 2006; Bloom & Lovejoy 2012). The family name Engraulidae literally means "small fish" in reference to the relatively small sizes of most Anchovies (<200 cm TL; Nelson 2006).

North American Engraulidae diversity is limited to 30 species found on both sides of the continent, and only 5 are recorded from fresh water. Because little information is available for these five species (see diversity and distribution section), this chapter largely focuses on *Anchoa mitchilli*, the Bay Anchovy ("anchoa" from Spanish "anchova," a herring-like fish; "mitchilli" after Samuel Latham Mitchill [1764–1831], an American naturalist). The Bay Anchovy is an important member of coastal and estuarine ecosystems along the eastern North American coast and throughout much of its range is the most abundant pelagic prey species available to predatory fishes (Hildebrand 1963). The species occurs in estuaries and river mouths consistently, but few far inland records are available. That said, Bay Anchovy are taken hundreds of kilometers upstream of the salt water–fresh water interface, warranting their inclusion here; however, no freshwater breeding populations are known.

Engraulidae is divided into two subfamilies, Coiliinae and Engraulinae, and occurs primarily in the Atlantic, Pacific, and Indian Oceans. Coiliinae contains 5 genera and 47 species that are confined to the Indo-Pacific region, and Engraulinae contains 11 genera and 92 species that occur in the Indo-Pacific region and the Western Hemisphere (Grande 1985; Whitehead et al. 1988; Kullander & Ferraris 2003; Nizinski & Munroe 2003; Nelson 2006; Bloom & Lovejoy 2012). Species are divided almost equally between the Indo-Pacific and Western Hemisphere regions: 71 species are recognized currently from the Indo-Pacific Ocean and 68 from the Atlantic and Eastern Pacific Oceans. Only two species (both in the genus *Engraulis*, subfamily Engraulinae) are known from the eastern Atlantic Ocean. The New World genus *Anchoa* is the most speciose (35 species), but genetic analyses indicate it is not monophyletic (Bloom & Lovejoy 2012). Other speciose genera are the Indo-Pacific genera *Thryssa* (24 species) and *Stolephorus* (19 species) (Whitehead et al. 1988; Nelson et al. 2004; Bloom & Lovejoy 2012). Most Anchovies live in tropical to warm-temperate marine waters; however, the genus *Engraulis* exhibits a modified anti-tropical (i.e., bipolar) distribution, occurring in disjunct northern and southern groups (Whitehead et al. 1988; Mecklenburg et al. 2002). However, we emphasize the genus *Engraulis* is not monophyletic (Bloom & Lovejoy 2012).

Although supporting fewer genera (seven), the Indo-Pacific region contains the greatest morphological diversity of Engraulidae. Probably the most extreme in this regard is

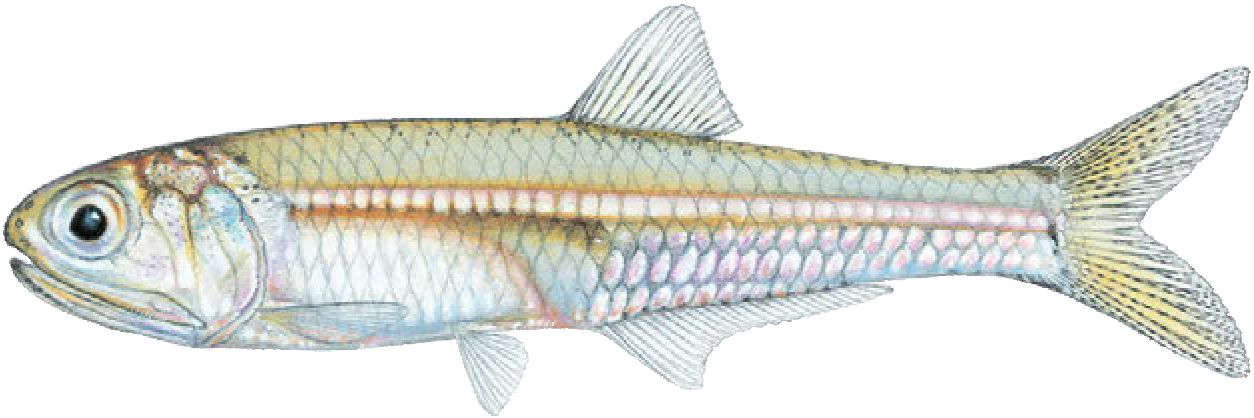


Plate 11.1. Bay Anchovy, *Anchoa mitchilli*, male

the genus *Coilia*, in which the anal fin is unusually long and confluent with the caudal fin, superficially resembling the unrelated freshwater fish family Notopteridae (Featherfin Knifefishes). Other examples of morphological diversity are seen in the genera *Coilia* and *Setipinna*, which have one or more long pectoral fin rays extending well back along the length of the anal fin, and in the genus *Thryssa*, which can have a spectacularly long maxillary bone that is lancet shaped and extends posteriorly past the base of the pelvic fin (Whitehead et al. 1988). The genera in the Atlantic and Eastern Pacific Oceans of the Western Hemisphere are morphologically conservative, being apparently subject to homoplasious morphologies (Bloom & Lovejoy 2012), and thus posing greater challenges to species identifications.

DIVERSITY AND DISTRIBUTION

A total of 5 genera and 30 Anchovy species occur in the Atlantic and Pacific Oceans of North America (Table 11.1). Of these, five species are known from fresh water: *Anchoa analis* (Longfin Pacific Anchovy) from the Eastern Pacific Ocean, and *Anchoa belizensis* (Belize Anchovy), *Anchoa hepsetus* (Striped Anchovy), *Anchoa mitchilli* (Bay Anchovy), and *Anchoa parva* (Little Anchovy) from the Western Atlantic Ocean. The Longfin Pacific Anchovy has a relatively restricted range along the Pacific Coast of Mexico and is a predominantly brackish water species that is unknown from strictly marine habitats (Whitehead et al. 1988). The Belize Anchovy has an equally restricted range in Belize, the southern coast of Yucatan, Mexico, and the outlet of Lake Izabal, Guatemala, and also is not known from strictly marine waters (Greenfield & Thomerson 1997). Ecological information for these two species is sparse, and little is known about them. The three remaining Anchovies recorded from fresh water in North America are all essentially classified as marine species. The Striped Anchovy and Little Anchovy occur occasionally in fresh waters in Mexico but are not recorded from fresh water in the United States even though they are found along the coasts (Nelson et al. 2004). The Bay Anchovy is the only known marine species of Engraulidae in North America that moves significant distances into fresh water. These migrations upstream are mostly into large tributaries of the Gulf of Mexico in the southeastern United States (Fig. 11.1). Because an abundance of information is available on the Bay Anchovy compared with that on the Belize Anchovy and Longfin Pacific Anchovy, and because the Striped Anchovy and Little Anchovy rarely occur in fresh water, the Bay Anchovy is the only species treated here (Table 11.2).

Anchoa mitchilli is abundant along the Atlantic and Gulf Coasts of the United States and Mexico. The Bay Anchovy ranges from Cape Cod, Massachusetts, south to Yucatan, Mexico (Morton 1989) (Fig. 11.1). Daly (1970) took it off Long Key, Florida, and suggested that Bay Anchovy are present throughout the Florida Keys, but others have stated that the species is apparently absent from this area

Table 11.1. Genera, diversity, range, and occurrence in fresh water of North American Engraulidae (Nelson et al. 2004). A = Atlantic Ocean, P = Pacific Ocean, AM = Atlantic Ocean of Mexico but not the United States or Canada, PM = Pacific Ocean of Mexico but not the United States or Canada.

Genus	Number of Species	Range	Occurrence in Fresh Water
Anchoa	23	A, P	Yes (5 species); no (18 species)
Anchovia	2	AM, PM	No
Anchoviella	1	A	No
Cetengraulis	2	AM, P	No
Engraulis	2	A, P	No

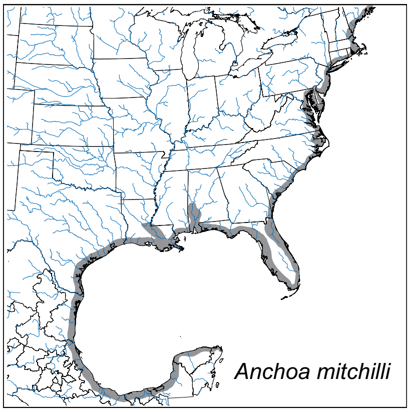


Figure 11.1. Geographic range of the Bay Anchovy, *Anchoa mitchilli*, in North America.

(Morton 1989). Although primarily marine and estuarine, this species regularly moves short distances into fresh water at mouths of rivers and streams. Most pertinent here are records of far-upstream movements by Bay Anchovy. In the Tombigbee River system (Mobile Basin), 99 Bay Anchovy were captured in 1986 from the Black Warrior River, Greene County, Alabama, 434 km upstream from strictly saltwater habitat (Mettee et al. 1996). In the same system, Bay Anchovy occur, often in large numbers, from lower reaches of the Tombigbee and Alabama Rivers and from smaller tributaries to Mobile Bay (Boschung & Mayden 2004). In the Mississippi River Basin, one individual was captured in 1976 from the Red River, Rapides Parish, Louisiana, 128 km upstream from its mouth to the Mississippi River (Tulane University Catalog #99194). In a survey of marine fishes in Virginia rivers (Massman 1954), Bay Anchovy commonly occurred in fresh water as both young and adults in the James, Chickahominy, Pamunkey, Mattaponi, and Rappahannock Rivers ≤64 km upstream of brackish water. The degree of freshwater penetration is highly irregular, and nothing is known about any possible genetic differences of these populations. Although records of far-upstream Bay Anchovy are few, the number of short-distance freshwater captures is plentiful. Freshwater reproduction is not documented.

Infraspecific Variability, Subspecies, and Clines

Hildebrand (1943) described two subspecies of Bay Anchovy, *Anchoa mitchilli mitchilli* and *Anchoa mitchilli diaphana*, splitting the overall range into a northern and a southern

Table 11.2. Life history traits of the Bay Anchovy, *Anchoa mitchilli*.

Trait	**Description**	**References**
Number of extant species	—	Valenciennes 1848
Salinity preference	Euryhaline (0–80 ppt), most common in ≤20 ppt	Burgess 1980; Morton 1989
Maximum size recorded in length and weight	102 mm TL; 3.5 g (?)	Jones et al. 1978; Castillo-Rivera et al. 1994
Maximum age	4 years	Bassista & Hartman 2005
Age and size at first reproduction	Young-of-the-year (2.5–3 months); ≥35 mm SL	Fives et al. 1986; Luo & Musick 1991
Iteroparous or semelparous	Iteroparous	Zastrow et al. 1991
Fecundity estimates (ovarian counts)	514–2,026 eggs/female/day, 45,110 eggs/female/season	Luo & Musick 1991; Zastrow et al. 1991
Egg deposition sites	Broadcast spawner	Peebles 2002
Ranges of spawning dates and temperature	May–August, up to year-round, >15°C	See Fig. 11.7
Habitat of spawning sites; average water depth	Estuaries: peak at 13–15 ppt and 20°C; <20 m deep	Jones et al. 1978
Incubation period; larval type at hatching	24 h at 25°C; proto-larva	Peebles 2002
Mean size at hatching	1.8–3.75 mm TL, 14 µg	Jones et al. 1978; Tucker 1989
Parental care	None	
Major dietary items	Copepods	See Fig. 11.9
General year-round habitat	Estuaries: <20 ppt and <20 m deep	Burgess 1980
Migratory or diadromous	Short inshore-offshore migrations; longer unknown	Morton 1989
Imperilment status	Stable	Warren et al. 2000

portion around South Carolina. *Anchoa m. diaphana* was distinguished from the nominate subspecies by a deeper and more strongly compressed body (23–26% of SL versus 19–21%), slightly fewer gill rakers on the lower limb of the first arch (21–23 versus 22–24), fewer vertebrae (38–41 versus 43–44), longer pectoral fins, and a narrower silvery lateral band (combined data of Hildebrand 1963 and Daly 1970). The range of *A. m. mitchilli* was described as from Cape Cod, Massachusetts, to South Carolina and that of *A. m. diaphana* from South Carolina to Yucatan, Mexico, with a zone of intergradation along the North Carolina and South Carolina coasts. These data were from specimens collected near the distributional extremes of the Bay Anchovy, and data from geographically intermediate populations revealed the differences as clinal (Burgess 1980). The number of vertebrae decreases from north (mode 42) to south (mode 40). The proportional length of the pectoral fin and body depth increases in more southern populations. In general, the depth of the body increases in proportion to SL from the northern to southern range extremes. Additionally, Bay Anchovy from northern populations on the upper Atlantic Coast seem to reach a slightly larger size than those to the south. Bay Anchovy from New York average 57.3 mm SL, but those from Yucatan only average 48.4 mm SL (Hildebrand 1943). Most contemporary workers do not recognize these subspecies.

Anchovies as Non-Natives

Throughout the 1940s and 1950s, numerous attempts were made to introduce Anchovies to California's Salton Sea, a saline rift lake near the U.S. border with Mexico. *Anchoa mundeoloides* (Northern Gulf Anchovy), *Cetengraulis mysticetus* (Anchoveta), and *Engraulis mordax* (Northern Anchovy), all West Coast Pacific Ocean species, were stocked intentionally as forage fishes. All three species were unsuccessful in creating viable populations and are extirpated from the Salton Sea (Fuller et al. 1999).

PHYLOGENETIC RELATIONSHIPS

Evidence supports recognition of the superorders Clupeomorpha and Ostariophysi as a sister-pair, together forming the subdivision Ostarioclupeomorpha that is sister to the Euteleostei (summarized by Nelson 2006). Although still under debate, the relationship between Clupeomorpha and Ostariophysi is generally accepted (see Li & Ortí 2007). Engraulidae is placed within the superorder Clupeomorpha along with 5 other families of "herrings or herring-like" fishes: Chirocentridae (Wolf Herrings, 1 genus, 2 species), Clupeidae (Herrings, 57 genera, 188 species), Denticipitidae (Denticle Herrings, 1 monotypic genus), Pristigasteridae (Longfin Herrings, 9 genera, 34 species), and Sundasalangidae (Sundaland Noodlefishes, 1 genus, 7 species) (Nelson 2006 and references therein). Clupeomorpha is based on several morphological characters, such as a unique otophysic (ear to swim bladder) connection, the second hypural fused at the base to the first ural centrum during all stages of development, and a single pelvic scute at the insertion of the pelvic fin (Grande 1985; Nelson 2006).

Clupeomorpha consists of one extant order, Clupeiformes, which can be divided into two suborders: Denticipitoidei and Clupeoidei. Fishes in Clupeiformes are unique in having a recessus lateralis (modification to the otophysic connection) (Nelson 2006), and monophyly is supported by other synapomorphies as well (Grande & Nelson 1985). Denticipitoidei contains a single family, Denticipitidae, and only one species *Denticeps clupeoides* (Denticle Herring) (Nelson 2006). The suborder Clupeoidei, composed of the remaining five Clupeomorpha families (Chirocentridae, Clupeidae, Engraulidae, Pristigasteridae, and Sundasalangidae), can be separated from Denticipitoidei by their lack of a body lateral line among other characters. The relationships among the Clupeoidei families are still largely unresolved. Di Dario (2002) hypothesized that the superfamilies Clupeoidea and Engrauloidea (= Engraulidae) are sister-groups based on shared morphological characters (cartilage chevrons at the tips of epicentrals, posteriorly directed parapophyses of the second vertebra, and interzygapophysal articulation). He also found evidence (gongyloid cartilage in the branchial arches) to support a close relationship between Pristigasteroidea and Engrauloidea (= Engraulidae) (Di Dario 2002); this was also the conclusion based on outer retina architecture (Heß et al. 2006). Di Dario (2009) revised his previous hypotheses and suggested that Chirocentridae is sister to Engraulidae based on the morphology of the suspensorium, branchial arches, and infraorbital bones. A consensus phylogram based on mitochondrial and nuclear DNA determined that Engraulidae was sister to all the remaining families of Clupeoidea (Fig. 11.2) (Li & Ortí 2007). This relationship is also supported by two whole mitogenome studies; however, the bootstrap support and Bayesian posterior probability is weak and susceptible to changes in analytical parameters (Lavoué et al. 2007; Lavoué et al. 2009). Monophyly of Engraulidae

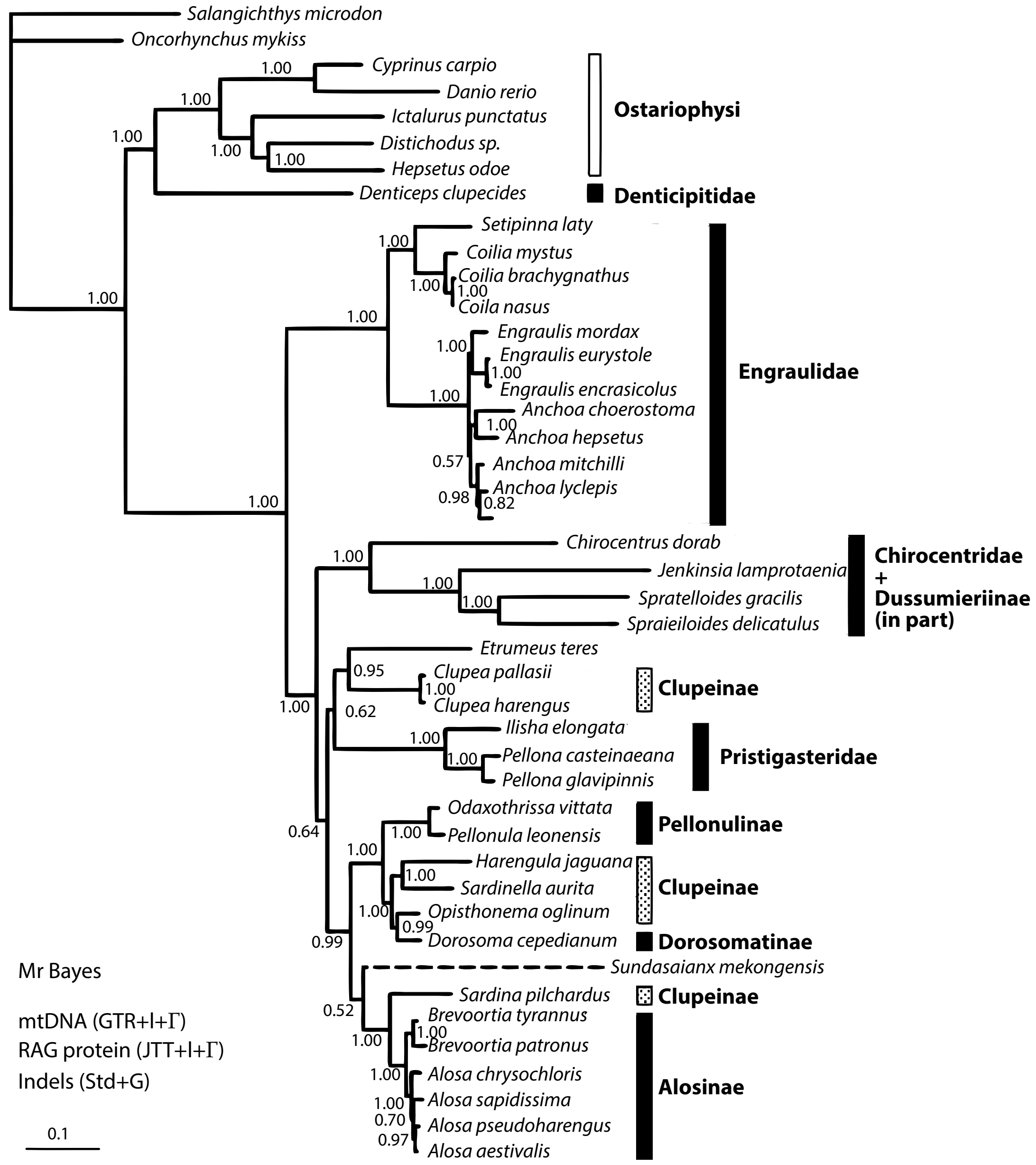

Salangichthys microdon
Oncorhynchus mykiss
1.00
Cyprinus carpio
Danio rerio
1.00
Ictalurus punctatus
1.00
Distichodus sp.
1.00
1.00
Hepsetus odoe
Denticeps clupecides
Ostariophysi
Denticipitidae
Setipinna laty
1.00
Coilia mystus
1.00
Coilia brachygnathus
1.00
Coila nasus
1.00
1.00
Engraulis mordax
1.00
Engraulis eurystole
1.00
Engraulis encrasicolus
1.00
Anchoa choerostoma
1.00
Anchoa hepsetus
0.57
Anchoa mitchilli
Anchoa lyclepis
0.98
0.82
1.00
Engraulidae
Chirocentrus dorab
1.00
Jenkinsia lamprotaenia
1.00
Spratelloides gracilis
1.00
Spraieiloides delicatulus
Chirocentridae + Dussumieriinae (in part)
Etrumeus teres
0.95
Clupea pallasii
1.00
Clupea harengus
1.00
0.62
Clupeinae
1.00
Ilisha elongata
1.00
Pellona casteinaeana
Pellona glavipinnis
Pristigasteridae
Odaxothrissa vittata
0.64
1.00
Pellonula leonensis
Pellonulinae
1.00
Harengula jaguana
1.00
Sardinella aurita
Clupeinae
1.00
Opisthonema oglinum
0.99
Dorosoma cepedianum
Dorosomatinae
0.99
Sundasaianx mekongensis
Mr Bayes
Sardina pilchardus
Clupeinae
0.52
Brevoortia tyrannus
mtDNA (GTR+I+Γ)
1.00
1.00
Brevoortia patronus
RAG protein (JTT+I+Γ)
Indels (Std+G)
1.00
Alosa chrysochloris
Alosinae
1.00
Alosa sapidissima
0.70
Alosa pseudoharengus
0.1
0.97
Alosa aestivalis

Figure 11.2. Consensus phylogram with mixed-model Bayesian analysis based on mtDNA, RAG protein sequences, and coded indels (see Li & Ortí 2007 for procedures). Posterior probabilities are indicated next to the nodes (redrawn from Li & Ortí 2007).

(Li & Ortí 2007; Lavoué et al. 2009; Bloom & Lovejoy 2012), Chirocentridae, and Pristigasteridae are supported (Grande 1985); however, monophyly of Clupeidae is not (Li & Ortí 2007).

Engraulidae is divided into two monophyletic subfamilies: Coiliinae and Engraulinae (Bloom & Lovejoy 2012). Some authors prefer to raise these subfamilies to family status (Coiliidae and Engraulidae) placed in the superfamily Engrauloidea (Di Dario 2009). Coiliinae have scutes present in front of and behind the pelvic fins. Scutes are absent in Engraulinae except for their occurrence in front of the pelvic fin in two genera (*Encrasicholina* and *Stolephorus*). The five genera of Coiliinae are *Coilia*, *Lycothrissa*, *Papuengraulis*, *Setipinna*, and *Thryssa*. The 11 genera of Engraulinae are *Amazonsprattus*, *Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Encrasicholina*, *Engraulis*, *Jurengraulis*, *Lycengraulis*, *Pterengraulis*, and *Stolephorus* (Grande 1985; Whitehead et al. 1988; Kullander & Ferraris 2003; Nizinski & Munroe 2003; Nelson 2006; Bloom & Lovejoy 2012). Evidence supports monophyly of these subfamilies (Li & Ortí 2007; Lavoué et al. 2009; Bloom & Lovejoy 2012). Within the Engraulinae, the genus *Engraulis* along with all other New World taxa form a monophyletic clade referred to as Engraulini (Fig. 11.3) (Lavoue et al. 2009; Bloom & Lovejoy 2012). A comprehensive molecular phylogeny using mtDNA indicated several genera in Engraulini are not monophyletic (e.g., *Anchoa*, *Engraulis*, *Anchovia*, *Anchoviella*, Bloom & Lovejoy 2012). The resulting phylogram (Fig. 11.3) places the Bay Anchovy as sister to the *Anchoa parva* (Little Anchovy) and *Anchoa delicatissima* (Slough Anchovy) clade (Bloom & Lovejoy 2012). Clearly, the phylogenetic arrangement based on molecular data (Fig. 11.3) differs significantly from the currently accepted taxonomy for New World Anchovies. The incongruence between the two suggests several genera are classified based on homoplasious morphological characters (e.g., deep body, numerous fine gill rakers) that may reflect aspects of the trophic niche rather than phylogenetic characters (Bloom & Lovejoy 2012).

FOSSIL RECORD

Anchovy fossils are incredibly scarce in comparison to those of other clupeomorph fishes. Fossil clupeid species alone number >100 species compared with only 2 skeletal fossil species that can be confidently classified as engraulids. The ecology of Anchovies likely is responsible for their lack of presence in the fossil record; extant species of Anchovies are predominantly near-shore marine fishes that live in habitats less likely to preserve skeletons. Additionally, more recent publications dispute the validity of many fossil species described in the past as engraulids. The oldest recognized Anchovy fossil species dates to the Miocene (23–5.3 mya) and, unlike other clupeomorphs, Anchovies are not known from the Eocene (55.8–33.9 mya) (Grande & Nelson 1985).

Numerous species are described from otoliths and fossils as belonging to Engraulidae. Otolith-described species include †*Anchoa nitida*, †*Coilia planate*, †*Setipinna retusa*, †*Stolephorus furculus*, and †*Stolephorus productus*. Some authors feel that classification based on otoliths alone is insufficient and that these species cannot be confidently included in Engraulidae (Grande & Nelson 1985); in contrast, Whitehead et al. (1988) recognized two otolith-based species (†*Anchoa nitida* and †*Setipinna retusa*). Seven species are described from fossil skeletons: †*Engraulis brevipinnis*, †*Engraulis evolans*, †*Engraulis longipinnis*, †*Engraulis macrocephalus*, †*Engraulis tethensis*, †*Engraulites remifer*, and †*Stolephorus lemoinei*. Grande & Nelson (1985) concluded that only two of these species are true Anchovies: †*Engraulis macrocephalus* Landini & Menesini 1978, from Calabria, Italy, of Pliocene-Pleistocene age (5.3–1.8 mya) and †*Engraulis tethensis* Grande & Nelson 1985, from Lyssi, Cyprus, of Late Miocene–Early Pliocene age (23–5.3 mya).

More recent fossil otolith material has been found from Mississippi River mudlumps in Louisiana. At least three species of Engraulidae were found and identified as *Anchoa* cf. *A. mitchilli* and species of *Engraulis* species. Radiocarbon determinations age the mudlumps to Late Pleistocene–Early Holocene age (about 15,500 years before present) (Stringer 1992).

MORPHOLOGY

Species of engraulids generally are relatively small with large mouths and overhanging conical snouts projecting beyond the mandible (Fig. 11.4). Sizes range from the minute *Amazonsprattus scintilla* (Rio Negro Pygmy Anchovy), an Amazonian freshwater species ≤ 20 mm SL, to the partially anadromous *Coilia nasus* (Japanese Grenadier Anchovy), a Western Pacific Ocean species reaching 410 mm SL (Whitehead et al. 1988). The mouth is probably the most distinctive Anchovy characteristic, easily separating them from their nearest relatives, the Herrings; the maxilla is extremely long, reaching behind the eye and even to the gill cover in some species (Mettee et al. 1996). Anchovies in North America have spineless median and short dorsal fins (12–17 rays), strongly forked caudal fins, relatively long anal fins (15–40 rays) placed under or far behind the dorsal fin origin, median pelvic fins placed under or in front of the dorsal fin origin, pectoral fins placed far anterior and low on the body, and no adipose fin (Hildebrand 1943). Anchovies have translucent flesh and a distinctive silvery stripe along the elongate body. They lack a body lateral line and scales are thin, cycloid, and deciduous. Anchovy abdomens are frequently compressed, resulting in a slight keel. Teeth are usually small but can be uneven and canine-like (Hildebrand & Schroeder 1928). The presence of scutes on the belly separates Old World species (present) from New World species (absent) (Boschung & Mayden 2004). The eyes are moderately large, generally placed forward on the head, and can have well-developed adipose tissue in adults (Hildebrand 1943). Gill rakers are long, slender, and numerous (Boschung & Mayden 2004). Anchovies have two unique skeletal features among Clupeomorphs: the oblique posterior inclination of the suspensorium and the projection in advance of the vomer by the mesethmoid bone that supports a paired rostral organ (Grande & Nelson 1985).

Bay Anchovy Morphology

The Bay Anchovy is a small, delicate fish reaching a maximum of 102 mm TL (Jones et al. 1978), but is rarely >100 mm TL (Newberger & Houde 1995). Like in other

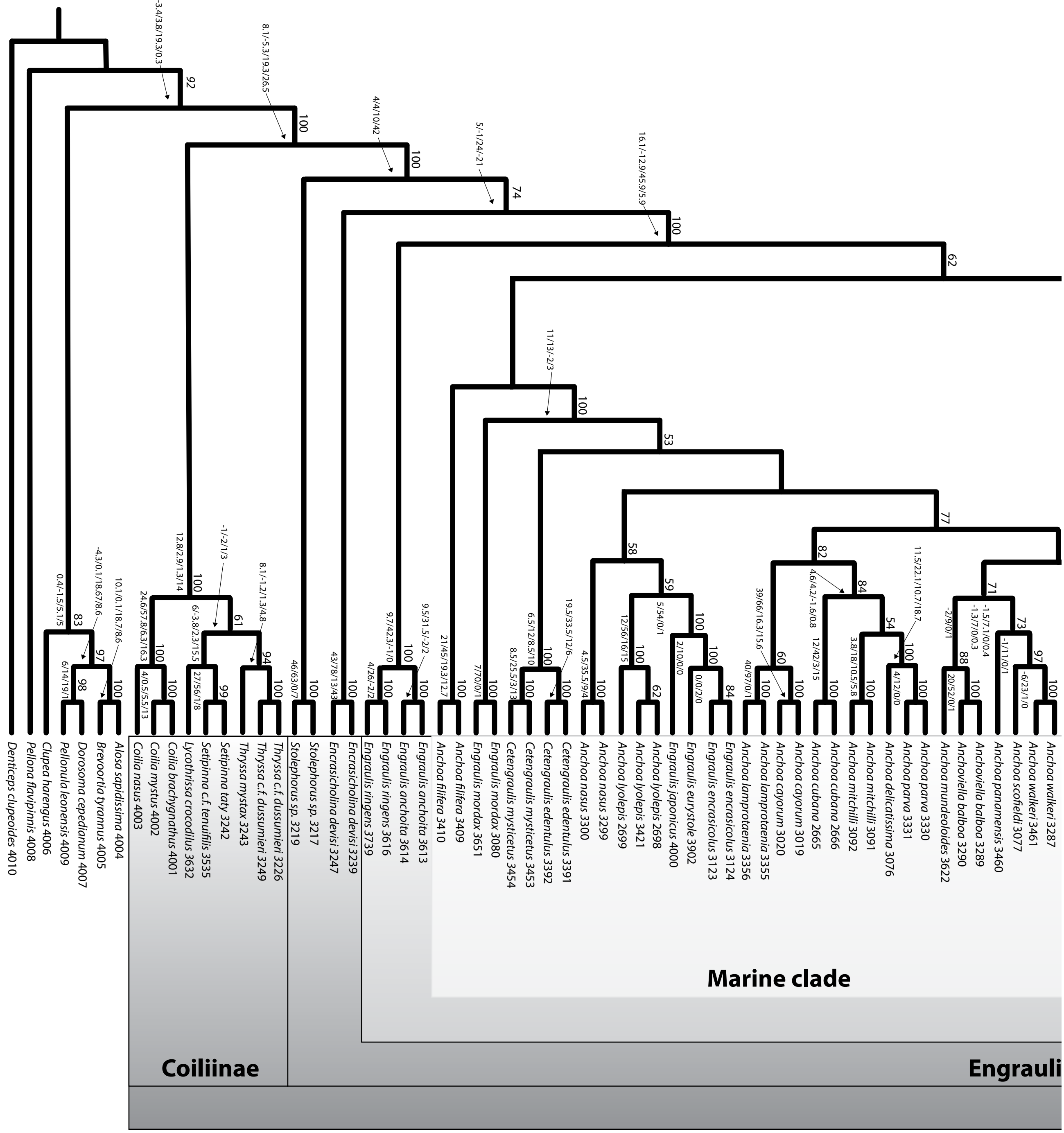
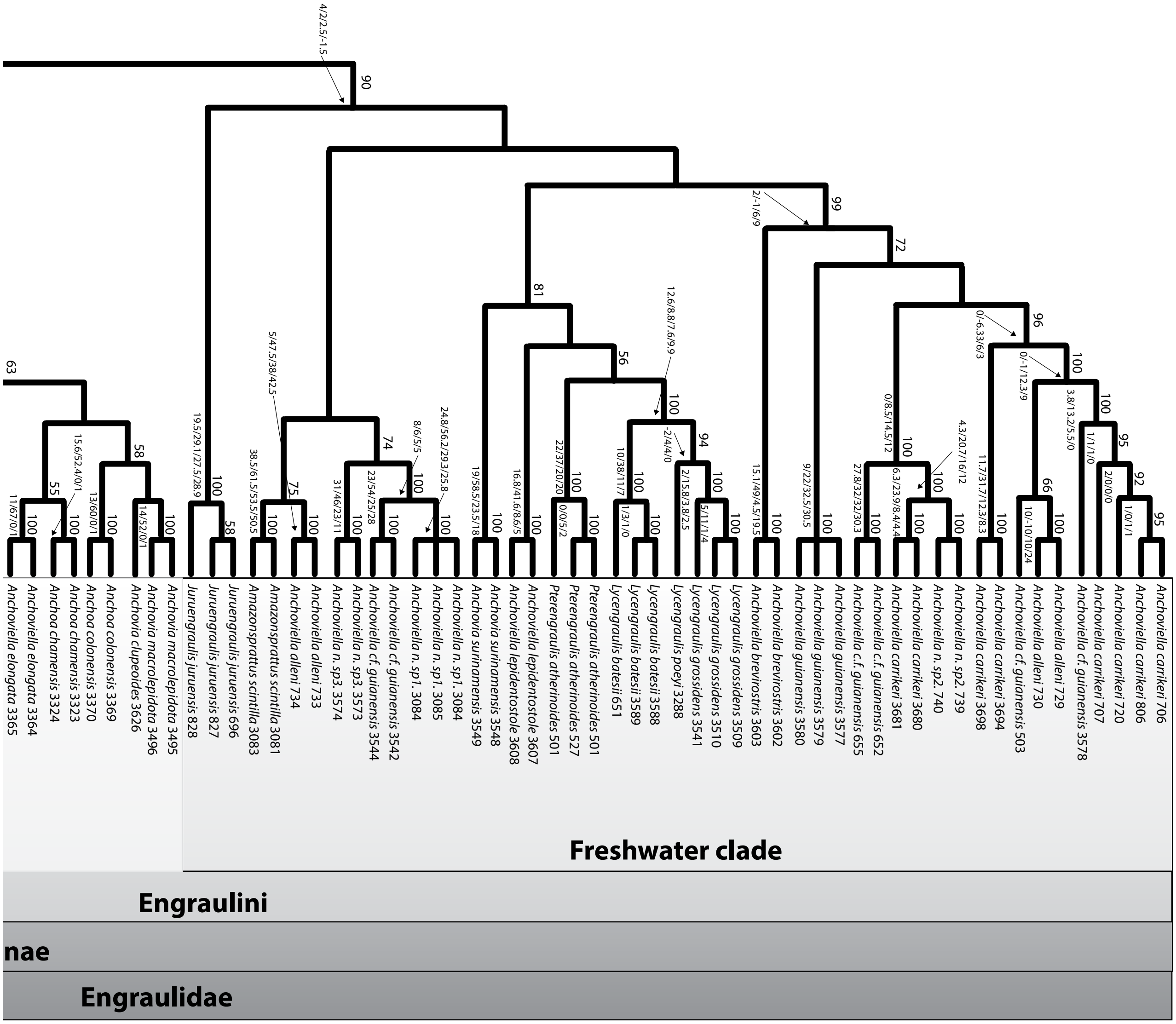

Denticeps clupeoides 4010
Pellona flavipinnis 4008
Clupea harengus 4006
Pellonula leonensis 4009
Dorosoma cepedianum 4007
Brevoortia tyrannus 4005
Alosa sapidissima 4004
Coilia nasus 4003
Coilia mystus 4002
Coilia brachygnathus 4001
Lycothrissa crocodilus 3632
Setipinna c.f. tenuifilis 3535
Setipinna taty 3242
Thryssa mystax 3243
Thryssa c.f. dussumieri 3249
Thryssa c.f. dussumieri 3226
Stolephorus sp. 3219
Stolephorus sp. 3217
Encrasicholina devisi 3247
Encrasicholina devisi 3239
Engraulis ringens 3739
Engraulis ringens 3616
Engraulis anchoita 3614
Engraulis anchoita 3613
Anchoa filifera 3410
Anchoa filifera 3409
Engraulis mordax 3651
Engraulis mordax 3080
Cetengraulis mysticetus 3454
Cetengraulis mysticetus 3453
Cetengraulis edentulus 3392
Cetengraulis edentulus 3391
Anchoa nasus 3300
Anchoa nasus 3299
Anchoa lyolepis 2699
Anchoa lyolepis 3421
Anchoa lyolepis 2698
Engraulis japonicus 4000
Engraulis eurystole 3902
Engraulis encrasicolus 3123
Engraulis encrasicolus 3124
Anchoa lamprotaenia 3356
Anchoa lamprotaenia 3355
Anchoa cayorum 3020
Anchoa cayorum 3019
Anchoa cubana 2665
Anchoa cubana 2666
Anchoa mitchilli 3092
Anchoa mitchilli 3091
Anchoa delicatissima 3076
Anchoa parva 3331
Anchoa parva 3330
Anchoa mundeoloides 3622
Anchoviella balboa 3290
Anchoviella balboa 3289
Anchoa panamensis 3460
Anchoa scofieldi 3077
Anchoa walkeri 3461
Anchoa walkeri 3287
Marine clade
Coiliinae
Engrauli

Figure 11.3. Phylogeny of the Anchovies (Engraulidae) based on a strict consensus of three equally parsimonious trees from fragments of mitochondrial (16s, cytochrome *b*) and nuclear (Rag1, Rag2) genes. Numbers above the nodes are bootstrap values from 1,000 replicates and numbers below indicate decay indices (redrawn from Bloom & Lovejoy 2002).

Anchovies, the short snout is conical, the mouth is large, and the maxillary is long and sharply pointed almost reaching the margin of the opercle. The dorsal fin (12–17 rays) lies above the anal fin (20–30 rays) and is closer to the caudal fin than the snout. The caudal fin is well forked, the anal fin long and narrow, the pelvic fins small and thoracic, and the pectoral fins jugular and placed low. The body is fusiform, strongly compressed, and covered


Anchoviella elongata 3365
Anchoviella elongata 3364
Anchoa chamensis 3324
Anchoa chamensis 3323
Anchoa colonensis 3370
Anchoa colonensis 3369
Anchovia clupeoides 3626
Anchovia macrolepidota 3496
Anchovia macrolepidota 3495
Juruengraulis juruensis 828
Juruengraulis juruensis 827
Juruengraulis juruensis 696
Amazonsprattus scintilla 3083
Amazonsprattus scintilla 3081
Anchoviella alleni 734
Anchoviella alleni 733
Anchoviella n. sp3. 3574
Anchoviella n. sp3. 3573
Anchoviella cf. guianensis 3544
Anchoviella cf. guianensis 3542
Anchoviella n. sp1. 3084
Anchoviella n. sp1. 3085
Anchoviella n. sp1. 3084
Anchovia surinamensis 3549
Anchovia surinamensis 3548
Anchoviella lepidentostole 3608
Anchoviella lepidentostole 3607
Pterengraulis atherinoides 501
Pterengraulis atherinoides 527
Pterengraulis atherinoides 501
Lycengraulis batesii 651
Lycengraulis batesii 3589
Lycengraulis batesii 3588
Lycengraulis poeyi 3288
Lycengraulis grossidens 3541
Lycengraulis grossidens 3510
Lycengraulis grossidens 3509
Anchoviella brevirostris 3603
Anchoviella brevirostris 3602
Anchoviella guianensis 3580
Anchoviella guianensis 3579
Anchoviella guianensis 3577
Anchoviella c.f. guianensis 655
Anchoviella c.f. guianensis 652
Anchoviella carrikeri 3681
Anchoviella carrikeri 3680
Anchoviella n. sp2. 740
Anchoviella n. sp2. 739
Anchoviella carrikeri 3698
Anchoviella carrikeri 3694
Anchoviella cf. guianensis 503
Anchoviella alleni 730
Anchoviella alleni 729
Anchoviella cf. guianensis 3578
Anchoviella carrikeri 707
Anchoviella carrikeri 720
Anchoviella carrikeri 806
Anchoviella carrikeri 706
Freshwater clade
Engraulini
nae
Engraulidae

with small, deciduous, cycloid scales (37–44 laterally). No lateral line is present on the body. The abdomen forms a sharp keel and is much more convex than the dorsum. Teeth are small, pointed, and present on both jaws. Gill membranes are largely separate and free from the isthmus; gill rakers are long and slender (20–26, lower limb first arch) (see Hildebrand & Schroeder 1928; Hildebrand 1943; Hildebrand 1963; Jones et al. 1978).

Pigmentation in live fish is translucent, greenish above with bluish reflections and silvery below. Bay Anchovy opercula, eyes, jaws, scales, and peritoneum are silvery. A silvery lateral stripe, narrower than the eye, extends from head to caudal base. In preserved specimens, the coloration is a light yellow above with the lower body and sides of the head silvery and with highly variable melanophore pigmentation (Jones et al. 1978). The dorsum has dusky

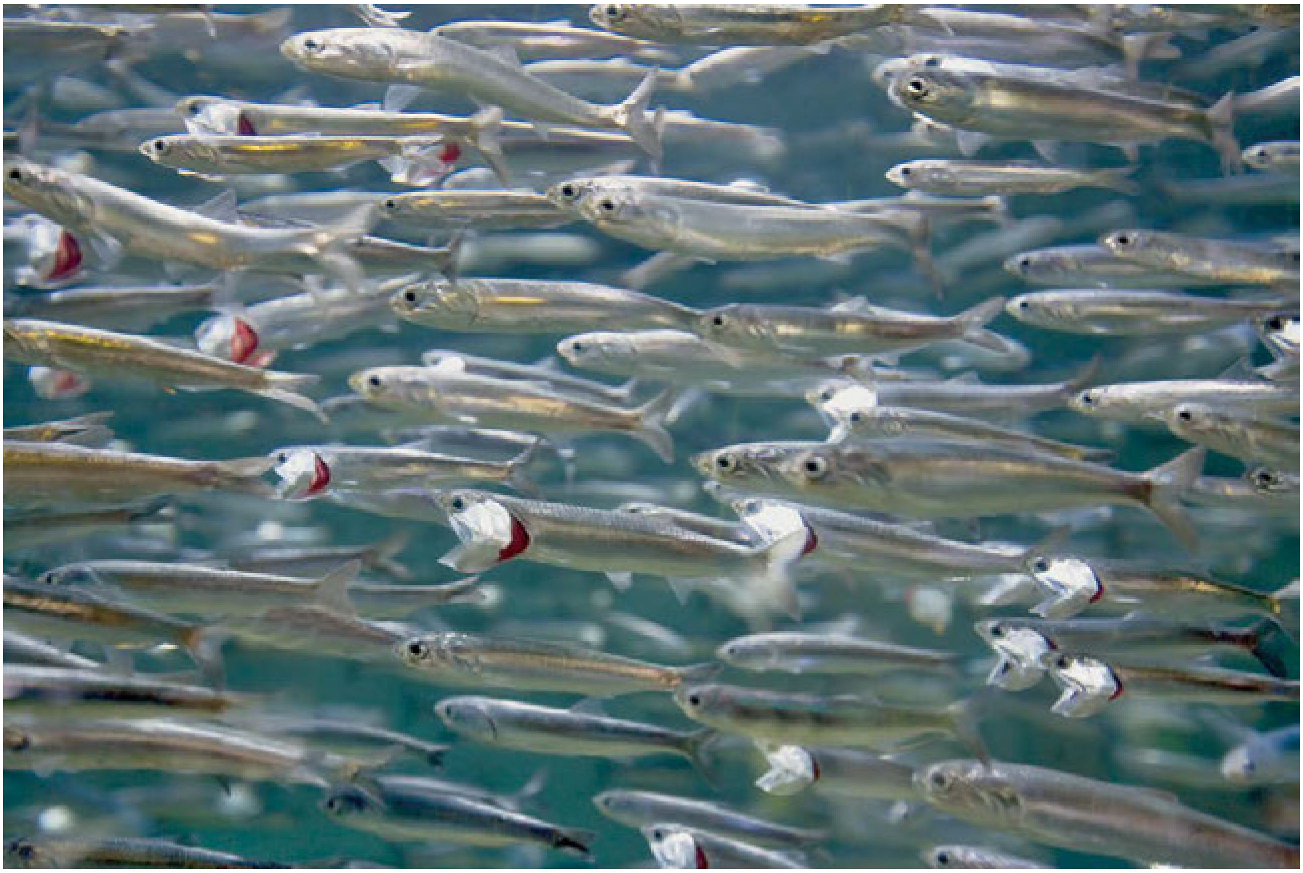


Figure 11.4. Photograph of *Engraulis mordax* (Northern Anchovy) schooling at the Oregon Coast Aquarium (photograph by and used with permission of ©Dennis Frates).

punctulations arranged in series, the base of the anal fin has dark dots that continue onto the caudal peduncle as a dark line, and the caudal has many dark points (Hildebrand 1943).

GENETICS

Genetic work on Engraulidae and Bay Anchovy is limited. Engraulids have diploid chromosome numbers ranging from 42 to 48 (genera *Anchoa*, *Coilia*, *Engraulis*, and *Thryssa*), and no Anchovies have chromosomes with second arms (Doucette & Fitzsimons 1988 and references therein). Bay Anchovy have 48 uni-armed chromosomes, and no sexual differences exist in karyotypes (see karyotype in Doucette & Fitzsimons 1988). The chromosomes cannot be identified accurately as homologous pairs because of the similarity in sizes and arm ratios between adjacent pairs in a size-graded series. The undifferentiated chromosome complement is also indistinguishable from three other Anchovies (*Coilia brachygnathus*, Yangtse Grenadier Anchovy; *Engraulis japonicus*, Japanese Anchovy; and Northern Anchovy) and two Herrings (*Alosa pseudoharengus*, Alewife, and *Alosa kessleri*, Caspian Anadromous Shad) (Doucette & Fitzsimons 1988).

Although Bay Anchovy may have distinct populations within their range (Hildebrand 1943), starch-gel electrophoresis of enzymes (21 loci) revealed high heterozygosity and little genetic structuring among populations in Chesapeake Bay. Bay Anchovy in this area also showed high levels of gene flow throughout the bay, suggesting mixing may occur during colder months when the fish aggregate in deeper waters (Morgan et al. 1995).

PHYSIOLOGY

Over their extensive range from Maine to Mexico (Fig. 11.1), Bay Anchovy encounter a range of environmental extremes. Even at small regional or local scales, the occurrence of the species in relatively shallow bays and estuaries increases its exposure to dynamic and often extreme environmental conditions. Perhaps unsurprisingly, they show incredible tolerance to extremes of temperature, salinity, and dissolved oxygen.

Temperature Tolerance

Across their extensive latitudinal range, Bay Anchovy are exposed to temperatures ranging from 2.2°C (Morton 1989) to 39.8°C (Robinette 1983). Estimates of the preferred temperatures for juveniles and adults range from 20 to 30°C (Houde & Zastrow 1991 as cited by Luo & Brandt 1993).

Salinity Tolerance

Bay Anchovy also are found over a wide range of salinities from fresh water (about 0 ppt) (Castillo-Rivera et al. 1994) to 80 ppt (Simmons 1957) and can be distributed independently of salinity (Weinstein 1979; Morton 1989; Martino & Able 2003). They are typically euryhaline and are most abundant in salinities <20 ppt (Burgess 1980), a value less than that of sea water (about 35 ppt). Spawning can occur at salinities >9 ppt (Morton 1989). Dovel (1981) observed peak larvae concentrations at <9.2 ppt, but eggs were observed at 5–28 ppt.

Dissolved Oxygen Tolerance

Most experiments on dissolved oxygen concentrations have focused on eggs and larvae. Bay Anchovy larvae are highly tolerant of low dissolved oxygen concentrations and have a threshold for survival at the 1–2 mg/l level. Larval survival after 24 h was 1% at 1 mg/l, 66% at 2.1 mg/l, and 80% at ≥3.1 mg/l (Breitburg 1994). Eggs can tolerate dissolved oxygen levels of 2.0 mg/l (MacGregor & Houde 1996 citing Houde & Zastrow 1991), but hatch rate declines significantly at levels <3 mg/l (Keister et al. 2000 citing Chesney & Houde 1989). Larval and adult Bay Anchovy actively avoid hypoxic water by moving up and down in the water column, and low dissolved oxygen levels are unlikely to cause mortality directly by exposure (Breitburg 1994). In the Neuse River Estuary, North Carolina, *Anchoa* spp. (25–85 mm TL) remained in water with dissolved oxygen (DO) >2.5 mg O_2 /l except when >70% of the water was hypoxic (DO < 2 mg O_2 /l), and some fish were in water with 1 mg O_2/l (Taylor et al. 2007).

Visual Structures and Photoreception

When compared with a typical vertebrate eye, the structure and arrangement of Anchovy cones is unusual (Fineran & Nicol 1978; detailed review by Heß et al. 2006). Evolutionarily, *Anchoa* developed polarized light detection over color vision. Although a few vertebrates can detect polarized light, some Anchovy species uniquely have clear-cut systems in place for it. The orientation of photoreceptors into cone units and associated guanine platelets in pigment cells allow polarization sensitivity. Detection of polarization may enhance zooplankton recognition from a distance, schooling behaviors, escape from predators, and navigation (Novales Flamarique & Hárosi 2002). Bay Anchovy larvae experience rapid eye development compared to two species of Clupeidae (*Brevoortia tyrannus*, Atlantic Menhaden, and *Harengula jaguana*, Scaled Sardine) (Higgs & Fuiman 1998), and visual acuity may be important to larval survival and feeding.

The photoreceptors consist of two normal rods and two unique cones; the cones lie in single vertical rows with rods between the rows. The two novel cone types are long cones with a wedge-shaped, cuneate outer segment and short cones, called bifid cones, with a bilobed outer segment (Fig. 11.5). The outer segments of both cones appear to be unique among vertebrates (Fineran & Nicol 1976). The two cone types form a structure called a cone unit that consists of two bifid cones sandwiching one long cone. Long and bifid cones alternate within a row and are staggered between adjacent rows that run vertically (dorso-ventrally) throughout the retina. The cone unit outer segments are isolated from each other by the pigment epithelium (Fig. 11.5) that contains stacks of melanosomes and guanine crystals, needles, and platelets forming a tapetum lucidum (see the following paragraph) (Fineran & Nicol 1978). The photoreceptor membrane lamellae also differ from a normal vertebrate eye in lying parallel, rather than transversely, to the long axis of the cell. Also unique to some Anchovies, the lamellae of long

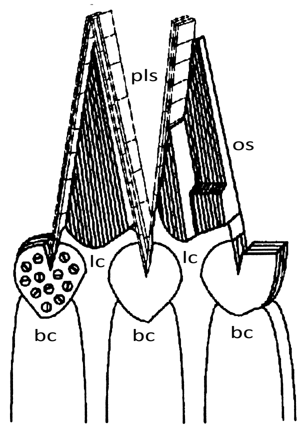


Figure 11.5. Schematic drawing of *Anchoa* cone structure: bc = bifid cone, lc = long cone, os = outer segment, pls = platelets (redrawn from Novales Flamarique & Hárosi 2002).

cones and bifid cones lie perpendicular to each other (Fineran & Nicol 1976). Rods, however, have the common transversely oriented lamellae seen in other vertebrates (Novales Flamarique & Hárosi 2002).

The tapeta lucida of teleosts is typically found in the pigment epithelium. For *Anchoa*, the tapetal material consists of stacks of guanine platelets or crystals arranged around the pigment epithelium cell processes and between photoreceptors (Fineran & Nicol 1977). Guanine tapeta are also found in Argentinidae (Argentines or Herring Smelts), Clupeidae (Herrings), Cyprinidae (Carps and Minnows), Elopidae (Tenpounders), Evermannellidae (Sabertooth Fishes), Malacanthidae (Tilefishes), Mormyridae (Elephantfishes), Percidae (Perches), Scopelarchidae (Pearleyes), and possibly Hiodontidae (Mooneyes) (Nicol et al. 1973). As noted, the guanine pigment epithelium covers the long cone outer segments and penetrates the lobes of the bifid cones (Fig. 11.5). The rods of *Anchoa* contain a typical vertebrate rhodopsin indicative of vitamin A_1-based pigments (Novales Flamarique & Hárosi 2002).

Hearing

Bay Anchovy are hearing specialists able to detect sound ≤4,000 Hz, although they cannot detect high-frequency sound (ultrasound) (Mann et al. 2001). Hence, unlike some clupeids (e.g., *Alosa sapidissima*, American Shad), the Bay Anchovy cannot detect the echolocation signals of predatory dolphins (Higgs 2004). The auditory bullae, which improve reception of acoustic stimuli, are fully inflated in Bay Anchovy larvae before they reach 4.55 mm TL, and this inflation occurs at an earlier ontogenetic stage than in Atlantic Menhaden (Higgs & Fuiman 1998).

Energetics

An energy budget was created using oxygen uptake, ingestion rates, and growth rates of laboratory-reared feeding larvae of Bay Anchovy (Table 11.3) (Houde & Schekter 1983). Mean oxygen uptake rates (µL individual^{-1} h^{-1}) for Bay Anchovy increased with age and weight: eggs 0.03, yolk-sac larvae (2 d) 0.07, (5 d) 0.24, (7 d) 0.57, and (12 d) 3.62. Larval Bay Anchovy have low assimilation (Table 11.3) efficiencies (A/I, 24–41%) and metabolism (M/I, 6–13%) that may be due to high excretion rates ((F + U)/I, 66–83%) (Houde & Schekter 1983). To compensate, Bay Anchovy larvae have to exceed minimum rations, feeding rates, and minimum prey levels (Table 11.3) to survive. Houde and Schekter (1983) hypothesized that Bay Anchovy try to maximize ingestion rate and may be prey limited due to low assimilation rates.

BEHAVIOR

Migration

Although Bay Anchovy move within estuaries and out onto the continental shelf, it is not known if long-distance migrations are undertaken. All sizes of Bay Anchovy vacate shallower waters for deeper waters in autumn and winter (Hildebrand 1963; Morton 1989), especially in the northern portion of the range. Some southern populations, however, remain abundant in estuaries year round (Vouglitois et al. 1987). North to south migrations are unknown, and Bay Anchovy apparently only have inshore-offshore migrations (Jones et al. 1978; Fives et al. 1986), probably cued by water temperature and season (Vouglitois et al. 1987).

Table 11.3. Energy budget (calories/day) and estimated minimum rations, feeding rates, and prey levels for larvae of Bay Anchovy, *Anchoa mitchilli*, at 10, 15, 20, 50, and 100 µg dry weight where I = G + M + U + F (see Houde & Schekter 1983 for methods; complied from that source).

	Larval Dry Weight (µg)				
Budget Component	**10**	**15**	**20**	**50**	**100**
Ingestion (I)	0.101	0.201	0.332	0.948	1.374
Growth (G)	0.021	0.031	0.041	0.103	0.206
Metabolism (M)	0.013	0.019	0.025	0.060	0.119
Urine (U)	0.007	0.014	0.023	0.066	0.096
Feces (F)	0.060	0.137	0.243	0.719	0.953
Assimilation (I-F)	0.041	0.064	0.089	0.229	0.421
Minimum rations (cal)	0.06	0.12	0.20	0.57	0.81
Minimum feeding rates (cal/h)	0.005	0.009	0.015	0.044	0.062
Minimum prey levels (number/l)	413	328	335	281	207

Multiple factors contribute to larval and juvenile fish migration and distribution. Bay Anchovy larvae remain in stasis or show weak up-river transport controlled by estuarine circulation and larval behaviors (Schultz et al. 2000). Some variables contributing to juvenile distribution are salinity, temperature, pH, dissolved oxygen, benthic structure, prey availability, and predator abundance (Taylor & Rand 2003).

Movement in some populations is cyclical across seasons and life stages. In early spring in the Hudson River Estuary juveniles and some adults move upstream to feed, by late spring mature fish move downstream to spawn in estuarine waters, newly hatched larvae move or are transported upstream to feed, and then, juveniles move downstream with the onset of colder weather (Dovel 1981) (Fig. 11.6). During the summer in Great Bay, New Jersey, it appears that larger Bay Anchovy (>50 mm FL) inhabit higher-salinity (29 ppt) and continental shelf habitats, while smaller fish (<50 mm FL) are more numerous in lower-salinity (8–29 ppt) and inland habitats (Martino & Able 2003). It is unknown if Bay Anchovy return to natal estuaries to spawn (Vouglitois et al. 1987).

Diel Activity

Assessment of the diel activity of Bay Anchovy varies by study with some populations showing diurnal activity, others showing nocturnal activity, and still others apparently responding to different environmental cues. Abiotic factors such as hypoxic water conditions and biotic factors such as prey abundance or predator presence can influence diel behavior (Taylor et al. 2007 and references therein). Bay Anchovy catch per unit effort in Barnegat Bay, New Jersey, averaged higher during the day than night over a 10-month period (March to December, Vouglitois et al. 1987). Bay Anchovy catches were also higher during the day, though not statistically different, than night throughout May to October in Caminada Pass, Louisiana (Sabins & Truesdale 1974). Conversely, at night Bay Anchovy were more abundant year round in Pueblo Viejo Lagoon, Mexico (Castillo-Rivera et al. 1994), and were in higher densities over the summer in the Neuse River Estuary, North Carolina (Taylor et al. 2007). Interestingly, abundance of Bay Anchovy in a small intertidal creek increased during the day with tidal flooding, but abundance did not increase if the same creek flooded at night. It was

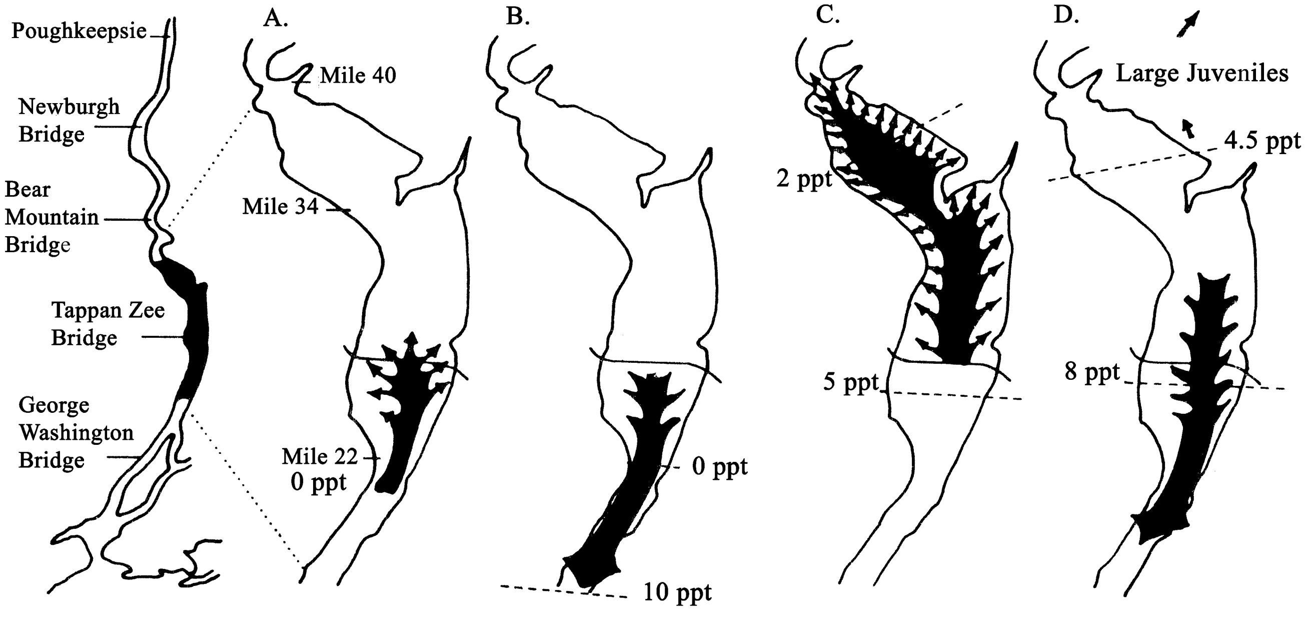


Figure 11.6. Cyclic movements of *Anchoa mitchilli* (Bay Anchovy) in the Hudson River estuary. (A) Migration of juveniles (possibly adults) into fresh water to feed as water temperatures approach 10°C in the early spring (May). (B) As water temperatures approach 15°C in the late spring and summer (June), sexually mature fish migrate to higher-salinity waters (>10 ppt). (C) Newly spawned larvae migrate upstream to low-salinity waters (<5 ppt) rich in food (June–August). (D) Large juveniles move farther upstream into fresh water (<4.5 ppt, August–September), while most of the age-0 fish remain in more saline waters. When water temperatures drop <10°C the juveniles move back downstream into higher-salinity waters (>8 ppt) (modified from Dovel 1981).

suggested that Bay Anchovy left the small intertidal creek at night to feed in the larger creek under less predation pressure, while during the day the small creeks provided refuge from predators (Reis & Dean 1981). Breitburg (1994) proposed that oxygen gradients play a role in vertical abundances of larvae in Chesapeake Bay. No clear diel pattern is known for Bay Anchovy over its geographical range, and diel activity is probably controlled locally by many variables.

Schooling

Anchovies are usually described as schooling fish (Fig. 11.4), but the literature available on their schooling behavior is limited. Because Anchovies lack lateral lines, vision probably plays a central role in schooling behavior (Luo 1993). Schools of Bay Anchovy form during the day and break up at night (Taylor et al. 2007), perhaps as a function of decreased vision at night. In southern Florida large mixed-species schools composed of Bay Anchovy, Bigeye Anchovy (*Anchoa lamprotaenia*), Dusky Anchovy, Flat Anchovy (*Anchoviella perfasciata*), Spanish Sardine (*Sardinella aurita*), *Harengula* spp. (Clupeidae), and *Jenkinsia* spp. (Clupeidae) form during the day in protected areas and disperse away from shore at night (Daly 1970). In Chesapeake Bay, juvenile and adult Bay Anchovy school during the day, and the school remains in a relatively fixed position. At night the school breaks up, and individuals become dispersed by the currents. In laboratory experiments, Bay Anchovy schools could maintain position against a current of 60 cm/s during daylight but only 53% of fish could maintain position at 5 cm/s in darkness (Luo 1993). This change in swimming speed and schooling was also observed in the Neuse River Estuary, North Carolina, under normal conditions; swimming speeds peaked around 1500 h, decreased after sunset, and increased again at dawn (Taylor et al. 2007). Under high density and stratified water (hypoxic) conditions fish maintained higher swimming speeds (10.7 body lengths/s) then when under low density or mixed water conditions (about 5 body lengths/s).

Foraging

Bay Anchovy generally are carnivorous planktivores foraging in shoals and channels of estuaries (Morgan 1990; see ecology section). Three types of feeding behaviors are used by Bay Anchovy: filter feeding on plankton items such as copepods; bottom feeding on larger items such as amphipods; and cannibalism (Din & Gunter 1986). Whether Bay Anchovy selectively capture organisms (Daly 1970; Odum & Heald 1972; Morton 1989; Johnson et al. 1990) or non-selectively strain water through the gill rakers (Din & Gunter 1986) when feeding on smaller prey items is debated. Larger food items are picked individually and can be actively fed on (Din & Gunter 1986). Once larval Bay Anchovy attack a prey item, they have a high overall capture rate (>70% in fish 4–8 mm SL) that increases with size and development (>95% in fish >14 mm SL), and larger larval fish also abort fewer attacks (<5% in 14–19 mm SL versus 33% in fish 4–8 mm SL) (Chesney 2008). Bay Anchovy display S-flex feeding in which the body is drawn into an S-shape from which a rapid strike is made at the food item (Detwyler & Houde 1970). Larval fish (3–19 mm SL) have a pause-travel search behavior where movements consist of a short pause to scan for prey items then either a burst to attack prey or flick (rotational) movement to scan a new field of view. As larval Bay Anchovy grow, the length of the searching time shortens (0.51–1.0 s at first feeding to 0.12–0.22 s at >9 mm SL) and attack speeds increase (0.39–0.62 body length/s for first feeding to 1.69 to 3.14 body lengths/s at 12 mm SL) (Chesney 2008). This foraging behavior is different from that observed in other larval clupeoid fishes (Chesney 2008 and references therein).

Diel or tidal periodicities in feeding and diet composition exist in some Bay Anchovy populations, but studies reveal feeding variability. In Biloxi Bay, Mississippi, Bay Anchovy had two feeding periods, a major peak at 0800 h and a minor peak just before 2400 h with little to no feeding between 1200 and 2200 h (Din & Gunter 1986). In North Inlet Estuary, South Carolina, Bay Anchovy showed a slightly different pattern; they fed primarily during the day and at high tide when compared with night and low tides (Johnson et al. 1990). Bay Anchovy can be primarily daytime feeders (Morgan 1990; Hartman et al. 2004); however, Daly (1970) tentatively concluded that they fed nocturnally in the currents. Diel changes in diet composition are also noted; more large prey were eaten around high tide at night and more small prey around low tide during the day, probably due to prey availability and abundances (DeLancey 1989; Johnson et al. 1990). One possible explanation for this variation could be related to physiochemical water conditions. In the Neuse River Estuary, North Carolina, species of *Anchoa* remained actively foraging at night when daily rations were not met due to hypoxic water conditions. At nighttime these fish displayed non-visual, perhaps filter-feeding behaviors different from daytime behaviors. Individual fish also made J- or V-shaped dives (<30 cm, 1–10 s in duration) into the hypoxic zone where prey concentrations were higher (Taylor et al. 2007).

REPRODUCTION

Sexual Maturity

The reported age of sexual maturity for Bay Anchovy varies. Several accounts describe early spring and summer spawned young-of-the-year Bay Anchovy reaching sexual maturity in 2.5–3 months and spawning that same season (Hildebrand & Cable 1931; Luo & Musick 1991). Sexual maturity is estimated to be obtained at 35–40 mm SL (Mansueti & Hardy 1967 citing Stevenson 1958). At Beaufort, North Carolina, young-of-the-year females contained well-developed ova (Hildebrand 1963), and in Chesapeake Bay fast summer growth of young-of-the-year allowed juveniles to reach spawning size in 80 days (Luo & Musick 1991). Several studies, however, have shown age-1 Bay Anchovy produce the majority of eggs (Peebles 2002 and references therein). Based on otolith-derived ages (Bassista & Hartman 2005), the Hudson River Estuary spawning stock contained mostly age-2 and age-3 fish; age-1 fish were virtually absent from the spawning stock. In sum, the spawning population of Bay Anchovy appears to vary by location and can be composed of young-of-the-year to age-4 fish.

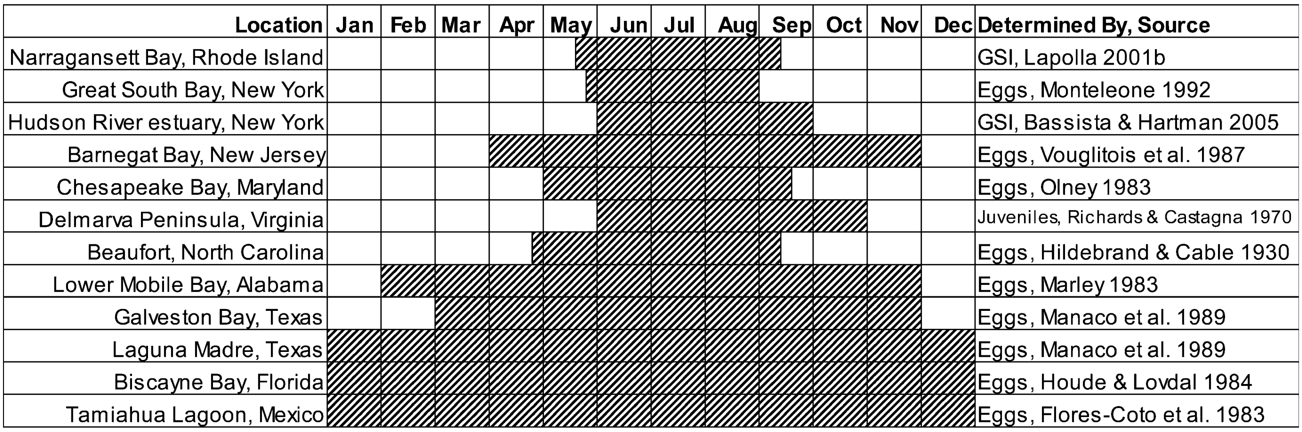
Spawning Cues and Seasonality

Environmental cues that induce Bay Anchovy spawning are unresolved. Spawning may be cued at least in part by water temperature (Zastrow et al. 1991). In Narragansett Bay, Rhode Island, spawning occurred when water temperatures were >15°C (Lapolla 2001b) and in Chesapeake Bay when water temperatures reached 17°C (Olney 1983). Others think temperature is an indirect measure of metabolic rate, primary production, or both (Peebles et al. 1996) that serve as direct cues. In support of this, peak spawning was correlated with larval food abundance but not salinity or temperature in Great South Bay, New York (Castro & Cowen 1991).

The length of the spawning season varies according to latitude with southern populations typically having longer spawning seasons (Fig. 11.7). In Great South Bay, New York, eggs occurred in bay waters from late May until August (Monteleone 1992), but eggs occurred year round in Tamiahua Bay, Mexico (Flores-Coto et al. 1983). The spawning season peaks even in populations with year-long reproduction; northern populations peak for 1–2 months in the summer (Monteleone & Duguay 1988), and southern populations peak for longer durations during spring and summer (Houde & Lovdal 1985).

Spawning Site

Bay Anchovy spawn in estuaries, river mouths, lagoons, harbors, sounds, and outer banks and on the continental shelf (Jones et al. 1978; Dovel 1981; Flores-Coto et al. 1983; Marley 1983; Witting et al. 1999); however, no freshwater spawning is known. Bay Anchovy typically spawn in water <20 m deep. Offshore spawning may exceed that of inshore when adults move offshore to feed at night during the spawning season (MacGregor & Houde 1996). Spawning can occur over a wide salinity range



Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Determined By, Source
Narragansett Bay, Rhode Island					▨	▨	▨	▨	▨				GSI, Lapolla 2001b
Great South Bay, New York					▨	▨	▨	▨					Eggs, Monteleone 1992
Hudson River estuary, New York						▨	▨	▨	▨				GSI, Bassista & Hartman 2005
Barnegat Bay, New Jersey				▨	▨	▨	▨	▨	▨	▨	▨		Eggs, Vouglitois et al. 1987
Chesapeake Bay, Maryland					▨	▨	▨	▨	▨				Eggs, Olney 1983
Delmarva Peninsula, Virginia						▨	▨	▨	▨	▨			Juveniles, Richards & Castagna 1970
Beaufort, North Carolina				▨	▨	▨	▨	▨	▨				Eggs, Hildebrand & Cable 1930
Lower Mobile Bay, Alabama		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		Eggs, Marley 1983
Galveston Bay, Texas			▨	▨	▨	▨	▨	▨	▨	▨	▨		Eggs, Manaco et al. 1989
Laguna Madre, Texas	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Eggs, Manaco et al. 1989
Biscayne Bay, Florida	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Eggs, Houde & Lovdal 1984
Tamiahua Lagoon, Mexico	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Eggs, Flores-Coto et al. 1983

Figure 11.7. Spawning season (shaded area) of the Bay Anchovy, *Anchoa mitchilli*, by location (listed north to south).

(1–37 ppt) but is estimated to peak around 13–15 ppt (Jones et al. 1978). Peak spawning water temperatures are >20°C (Jones et al. 1978), but spawning can begin as water reaches 12°C (Dovel 1981). Egg densities correlate positively with zooplankton and food amounts (Dorsey et al. 1996; Peebles et al. 1996; Peebles 2002). Areas with abundance of adult food items may be chosen preferentially for spawning (Luo & Musick 1991).

Spawning

Bay Anchovy are iteroparous broadcast spawners (Peebles 2002) that can spawn nightly during the peak period (Zastrow et al. 1991) and rapidly produce ova. Spawning occurs in large schools (Kuntz 1915). Oocytes >0.15 mm only occur during the spawning season; vitellogenesis occurs in oocytes >0.25 mm. During the peak spawning period, oocytes can hydrate and develop from 0.35 to 0.90 mm (spawning size) in 24 h. Hydration consists of oocytes rapidly absorbing fluids (4–14 h) of lower specific gravity than sea water and yolk granules fusing into yolk plates (Luo & Musick 1991; Bassista & Hartman 2005). Spawning occurs nightly at about the same time (Kuntz 1915) with high fertilization rates (94–100%) (Peebles 2002). Spawning typically starts between 1800 and 2100 h (e.g., 1800 h, Beaufort, North Carolina, Kuntz 1915; 2000 h, Manatee River Estuary, Florida, Peebles 2002; 2000 h in Hudson River Estuary, New York, Bassista & Hartman 2005; 2100 h in Barnegat Bay, New Jersey, Vouglitois et al. 1987). Nightly timing also can be dynamic in the same estuary as summer progresses. Bay Anchovy in Chesapeake Bay started spawning at 2000 h in June, 2100 h in July, and 2300 h in August (Luo & Musick 1991). Nightly spawning duration is typically 1–4 h (Luo & Musick 1991; Zastrow et al. 1991; Peebles 2002) but can last ≤10 h (Bassista & Hartman 2005). Bay Anchovy can spawn >50 times in a season. Almost all Bay Anchovy females in Chesapeake Bay apparently spawned nightly for about 50 nights during the peak period in 1986–1987 (Zastrow et al. 1991).

Fecundity, Egg Densities, and Reproductive Allocation

Bay Anchovy are highly fecund and can be the most abundant taxon of fish eggs and larvae collected in estuaries (Dovel 1981; Olney 1983; Leak & Houde 1987). Mean batch fecundity (eggs/spawn) ranges from 429 to 1,186 in Lower York River, Chesapeake Bay (Luo & Musick 1991), and from 514 to 2,026 in Patuxent River, Chesapeake Bay (Zastrow et al. 1991). Relative batch fecundity (eggs spawn^{-1} g^{-1} ovary-free female body weight) ranged from 334 to 803 (Luo & Musick 1991) and 441 to 959 (Zastrow et al. 1991) in the same studies. In the Hudson River Estuary, the mean relative batch fecundity was 506 with mean batch fecundities of 1,233 in 1996 and 1,508 in 1997 (Bassista & Hartman 2005). Length and weight of Bay Anchovy females are correlated positively with batch fecundity (Luo & Musick 1991; Wang & Houde 1994; Bassista & Hartman 2005). A linear regression model ($r^2 = 0.70$) predicted batch fecundity (hydrated oocytes per batch) of about 750 for a 1 g female (ovary-free body weight), 1,500 for a 2 g female, and 2,250 for a 3 g female (Luo & Musick 1991). Adult prey availability may affect egg production and fecundity (Peebles et al. 1996; Peebles 2002).

Egg densities >200 eggs/m^3 occur during spawning, peak at 1,098 for Great South Bay, New York (Monteleone 1992), range from 0.64 to 30.77 seasonally in Biscayne Bay, Florida (Houde & Lovdal 1984), range from 32 to 140 with a peak of 800 in Chesapeake Bay (Olney 1983), and range from 5 to 132 during peak spawning in Barnegat Bay, New Jersey (Vouglitois et al. 1987). Overall estimates of 45,110 eggs female^{-1} season^{-1} (Luo & Musick 1991) and 4.25×10^{12} (June 1993) to 8.43×10^{12} (July 1993) eggs/day baywide (Chesapeake Bay, Rilling & Houde 1999) provide insight into how fecund Bay Anchovy really are.

Gonad somatic indexes (GSI, gonad weight / gonad-free body weight × 100) are highest in the spring and summer during the Bay Anchovy spawning season and rapidly decline afterward. In Chesapeake Bay males have higher GSI than females (Zastrow et al. 1991); this may be true for all populations because males have larger gonads than females of the same body weight (Wang & Houde 1994). From February to November in Chesapeake Bay, GSI ranged from 0.47 to 7.40% for females and from 0.13 to 10.95% for males. During peak spawning season, females averaged 4.44% and males 7.18% (Zastrow et al. 1991). Female GSI ranged from 5.74 to 17.13% and male GSI from 6.06 to 15.09% during the spawning season (June–September) in the Hudson River Estuary (Bassista & Hartman 2005). The differences for these two estuaries may be because Zastrow et al. (1991) used Bay Anchovy >40 mm FL and Bassista and Hartman (2005) used individuals >60 mm TL for their analyses.

Embryonic Development

Bay Anchovy eggs occur throughout the water column at salinities of 8–15 ppt, tend to concentrate near the surface at salinities of 30–35 ppt, and remain buoyant until hatching (Jones et al. 1978; Morton 1989). This is a function of egg buoyancy since buoyancy decreases at low salinities and eggs remain buoyant at salinities >14 psu (= 14 ppt) (Peebles 2002).

Fertilized eggs of Bay Anchovy are relatively small, transparent, and planktonic; lack oil globules; and contain little yolk material (Kuntz 1915; Jones et al. 1978). Yolk that is present is separated into large masses appearing as big broken cells (Fig. 11.8). The eggs are slightly elongate; the major axis ranges from 0.65 to 1.33 mm long; and the minor axis is 0.1–0.3 mm shorter (Kuntz 1915). Egg size decreases with increasing water salinity and as the spawning season progresses (Jones et al. 1978). Eggs weigh 15 µg (Tucker 1989). Development of Bay Anchovy eggs (detailed by Kuntz 1915) is not different from development of typical pelagic teleostean eggs.

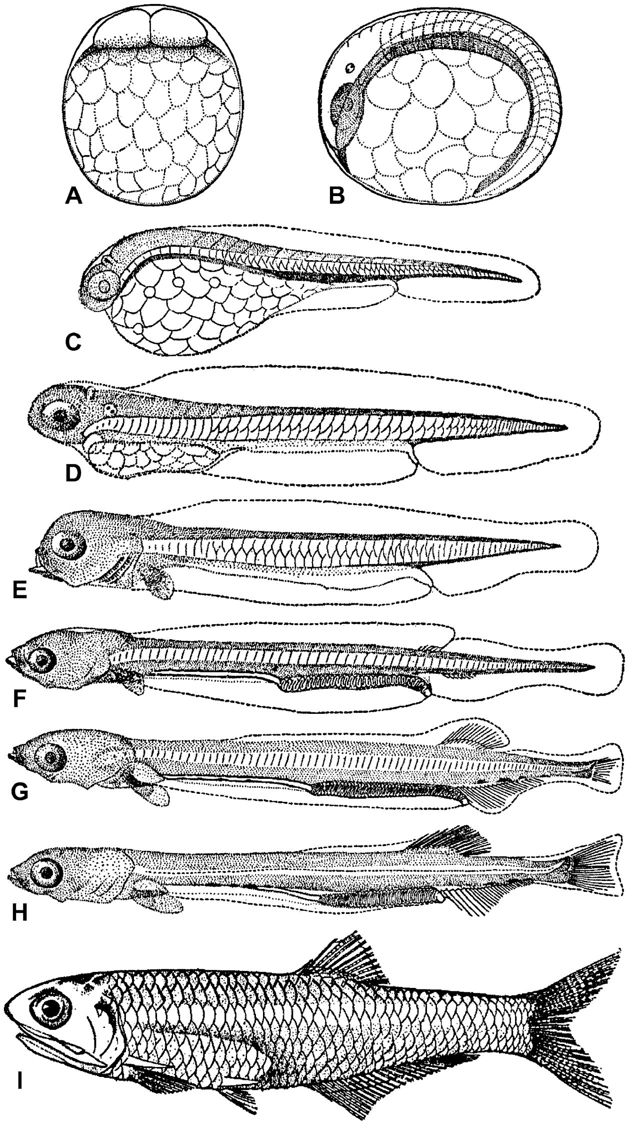


Figure 11.8. Embryonic and larval development of the Bay Anchovy, *Anchoa mitchilli*. (A) Egg with two-celled blastoderm and yolk (X60). (B) Egg with embryo curved around the yolk (X60). (C) Newly hatched larvae, 1.9 mm TL. (D) 12-h post-hatch larvae, 2.7 mm TL. (E) 3.4 mm TL. (F) 5 mm TL. (G) 7.5 mm TL. (H) 10.0 mm TL. (I) Adult fish, 7 cm TL (modified from Kuntz 1915).

Development and hatching times are relatively rapid. The egg is in the late morula stage (≥16 cells) 5 h after fertilization. At 10 h the blastopore closes, the embryo is >0.5 of the egg circumference, and it lies parallel with the major axis of the egg. Up to hatching, the embryo keeps elongating and can extend around the entire circumference of the yolk (Fig. 11.8) (Kuntz 1915). Hatching time varies slightly with temperature: 24 h at 27°C (Kuntz 1915; Jones et al. 1978), 23–24 h at 25°C (Peebles 2002), and 24–27 h at 24–25°C (Fives et al. 1986). At hatching, the larvae are long and slender, weigh 14 µg, are 1.8–3.75 mm TL, and have a posterior anus; the large, segmented yolk tapers to a point posteriorly (Jones et al. 1978; Tucker 1989). The head is deflected downward over the yolk, the body is flattened and slender, the fin fold is continuous, and no pigmentation is evident (Fig. 11.8) (Kuntz 1915).

Larval Development

Bay Anchovy larvae are abundant in estuaries and adjoining fresh water, and larvae may experience upriver or tidal transport upstream (Dovel 1981; Kimura et al. 2000; Schultz et al. 2003). They also are found at all sizes offshore (MacGregor & Houde 1996). Larvae might demonstrate diel behavior, being more abundant near the surface at night (Schultz et al. 2003).

Larvae must develop rapidly due to the small amount of yolk available (Table 11.4; Fig. 11.8). The yolk is absorbed completely in the first 27–52 h after hatching, occurring faster at higher temperatures (Houde 1974; Tucker 1989). Larvae are vulnerable to food shortages during the second and third days after hatching (Kuntz 1915; Tucker 1989). Larvae differ from adults in that they are slender; have a terminal mouth; have a short, round maxillary; and are mostly transparent because they lack pigment (Hildebrand & Schroeder 1928). Bay Anchovy do not have positive growth until after the yolk sac is absorbed completely (Tucker 1989) and quickly develop into adults within 2.5–3 months (Table 11.4).

Table 11.4. Bay Anchovy, *Anchoa mitchilli*, larval and juvenile development by length (TL, unless otherwise stated) and age post-hatch (h, hours).

Larval Length/Age	Development	References
27–32 h	Eye pigmentation	Leak & Houde 1987; Tucker 1989
27–52 h	Yolk completely absorbed	Leak & Houde 1987; Tucker 1989
2.6–2.8 mm	Head no longer deflected down; yolk elongated along body	Kuntz 1915
2.7 mm, 36 h	Mouth terminal and apparently functional; anlage of pectoral present; first daily otolith ring created	Kuntz 1915; Jones et al. 1978; Leak & Houde 1987
2.9 mm	Fin fold somewhat constricted in caudal region	Jones et al. 1978
44 h	First feeding	Leak & Houde 1987
102–122 h	Starvation (with no food provided)	Leak & Houde 1987; Tucker 1989
3.7 mm	Incipient rays in caudal fin; few chromatophores between anal and caudal fin and along midline below gut	Jones et al. 1978
5 mm	Incipient rays in caudal and anal fins; muscular rings developed along hindgut; intestine convoluted	Kuntz 1915; Jones et al. 1978
7.5 mm	Urostyle oblique	Jones et al. 1978
7–8 mm	Some with full dorsal and anal fin counts; chromatophores along ventral aspect of thoracic region and at base of caudal fin	Kuntz 1915; Jones et al. 1978
11–12 mm	Full dorsal and anal fin counts	Jones et al. 1978
15.5 mm SL	Metamorphosis into juveniles begins	Jones et al. 1978
19.5 mm	Chromatophores between operculum and pelvic fins, anal to caudal fins, midlateral row on dorsolateral surface, dark blotch between eyes on top of head, and caudal fin heavily pigmented	Jones et al. 1978
20–25 mm	Projecting snout; body depth increases from 9 times in body depth to 5.5 times	Jones et al. 1978; Morton 1989
22.5 mm SL	Metamorphosis into juveniles essentially complete	Jones et al. 1978
34–40 mm	Minimum length at maturity (2.5 months)	Jones et al. 1978
43 mm	Row of chromatophores along anal base and onto caudal fin, a few on the head	Jones et al. 1978
60 mm	Adult characteristics present	Houde 1974

Mating System

Bay Anchovy are iteroparous broadcast spawners with high fecundities. Spawning energy is derived from daily feeding, not energy stores (Luo & Musick 1991; Wang & Houde 1994). Peebles et al. (1996) described Bay Anchovy in Tampa Bay, Florida, as an income breeder in which seasonal and spatial patterns in egg production can be explained by adult metabolic rate and ration. This fish produces daily cohorts of eggs and larvae in great abundances that in turn experience rapid growth along with high mortality (MacGregor & Houde 1996). Bay Anchovy are therefore strongly r-selected and well adapted to persist in the dynamic estuarine habitats in which they reside (Lapolla 2001a). They also are described as opportunistic life history strategists because of their early maturation, batch spawning, rapid larval growth, and rapid population turnover (Rose et al. 1999).

ECOLOGY

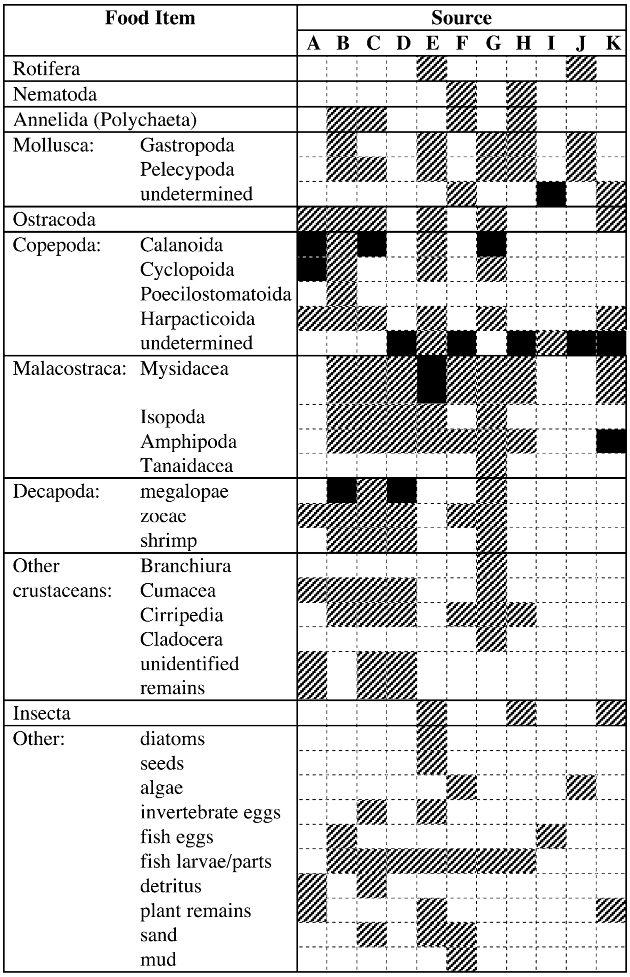
Habitat

Bay Anchovy occupy diverse coastal habitats of the United States and Mexico primarily because of their high tolerances of varying salinity and temperature. They typically live in shallow water (<20 m deep) but occur at depths ≤36 m (Burgess 1980). Bay Anchovy are euryhaline and occur in estuarine, coastal, and freshwater habitats, including bays, sounds, bayous, salt marshes, lagoons, sandy beaches, surf zones, sea grass beds, muddy coves, grassy areas along beaches, intertidal creeks, river mouths, mangrove forests, artificial canals and waterways, coastal rivers, backwaters, and offshore waters (Dahlberg & Odum 1970; Odum & Heald 1972; Carr & Adams 1973; Jones et al. 1978; Kinch 1979; Burgess 1980; Modde 1980; Castillo-Rivera et al. 1994; Griffith & Bechler 1995). Substrate type and vegetation have little effect on Bay Anchovy distribution (Killgore et al. 1989; Morton 1989; Castro & Cowen 1991), although fewer Bay Anchovy were found in vegetated than unvegetated backwaters in Texas (Griffith & Bechler 1995). In freshwater rivers of Alabama, most Bay Anchovy occurred along the margins of aquatic vegetation and tree limbs when sampling with boat-mounted electrofishers and over clean sand and gravel when sampling with seines (Mettee et al. 1996).

Diet

Bay Anchovy are primarily zooplanktivores but also consume larger prey items when available (Fig. 11.9). Copepods are the major food item in most populations, but other prey like mysids, amphipods, crab megalopae, and mollusk veligers also can dominate the diet. Diet is determined largely by prey availability; Bay Anchovy are opportunistic and can rapidly switch prey types accordingly (Johnson et al. 1990).

Ontogenetic changes in diet may exist in some populations of Bay Anchovy. In model simulations calibrated by empirical data, the fish fed on larger zooplankton as fish size increased (Rose et al. 1999). Larvae (3.4 mm TL) begin feeding on organisms 50–112 μm wide (Detwyler & Houde 1970), and adults primarily eat organisms 0.22–1.17 mm wide (0.3–12 mm long) (Johnson et al. 1990). Copepods, a major food item, usually are consumed at various life stages and sizes as Bay Anchovy grow (Peebles et al. 1996). In Lake Pontchartrain, Louisiana, two feeding stages occurred. Small, young fish (35–40 mm SL) were plankton strainers and fed mostly on microzooplankton (e.g., rotifers and copepods). Large, older fish (60–65 mm SL) fed more selectively on macrozooplankton (e.g., small shrimp and fishes, primarily larval clupeids and engraulids), bottom-dwelling mollusks, and crustaceans (Darnell 1958). Ontogenetic diet shifts also occurred in Bay Anchovy in North River, Florida. Larval and juvenile fish (<25 mm SL) fed solely on microzooplankton, and adults (31–62 mm SL) fed primarily on larger items like amphipods and mysids (Odum & Heald 1972). Conversely, no ontogenetic changes in diet were noted for populations in Apalachee Bay, Florida (Livingston 1982), or Hudson River, New York (Hartman et al. 2004).



Food Item		Source										
		A	B	C	D	E	F	G	H	I	J	K
Rotifera						▨					▨	
Nematoda							▨		▨			
Annelida (Polychaeta)			▨	▨			▨		▨			
Mollusca:	Gastropoda		▨			▨		▨	▨		▨	
	Pelecypoda		▨	▨		▨		▨	▨		▨	
	undetermined						▨			■		▨
Ostracoda		▨	▨	▨		▨		▨				▨
Copepoda:	Calanoida	■	▨	■		▨		■				
	Cyclopoida	■	▨			▨		▨				
	Poecilostomatoida		▨									
	Harpacticoida	▨	▨	▨		▨		▨				▨
	undetermined				■	▨	■		■	▨	■	■
Malacostraca:	Mysidacea		▨	▨	▨	■	▨	▨	▨			▨
	Isopoda		▨	▨	▨	▨		▨				
	Amphipoda		▨	▨	▨	▨	▨	▨	▨			■
	Tanaidacea							▨				
Decapoda:	megalopae		■	▨	■			▨				
	zoeae	▨	▨	▨	▨		▨	▨				
	shrimp		▨	▨	▨			▨				
Other crustaceans:	Branchiura							▨				
	Cumacea	▨	▨	▨	▨			▨				
	Cirripedia		▨	▨	▨		▨	▨	▨			
	Cladocera							▨				
	unidentified remains	▨		▨	▨							
Insecta						▨			▨			▨
Other:	diatoms					▨						
	seeds					▨						
	algae						▨				▨	
	invertebrate eggs			▨		▨						
	fish eggs		▨							▨		
	fish larvae/parts		▨	▨	▨	▨	▨	▨	▨			
	detritus	▨		▨								
	plant remains	▨				▨						▨
	sand			▨		▨	▨					
	mud						▨					

Figure 11.9. Recorded food items of the Bay Anchovy, *Anchoa mitchilli* (shaded = recorded; black = most abundant). Sources: (A) Apalachee Bay, Florida, Livingston (1982); (B) North Inlet Estuary, South Carolina, Johnson et al. (1990); (C) Tampa Bay, Florida, Peebles et al. (1996); (D) Folly Beach, South Carolina, DeLancey (1989); (E) Lake Pontchartrain, Louisiana, Darnell (1958); (F) Marco Island, Florida, Kinch (1979); (G) Biloxi Bay, Mississippi, Din & Gunter (1986); (H) Hudson River, New York, Hartman et al. (2004); (I) Crystal River, Florida, Carr & Adams (1973); (J) Biscayne Bay, Florida, Houde & Lovdal (1984); (K) North River, Florida, Odum & Heald (1972).

Growth and Longevity

Bay Anchovy are small, short-lived fish that experience rapid growth. The maximum size recorded is 102 mm TL (Jones et al. 1978), average size is 50–75 mm TL (Morton 1989; Hagan & Able 2003), and northern populations typically grow larger than southern populations (Hildebrand 1963). The maximum recorded age for a Bay Anchovy is 4 years old (otolith-based; Bassista & Hartman 2005), but the majority of any given population consists of young-of-the-year and age-1 fish (Newberger & Houde 1995).

Temperature extremes and food availability are primary determinants of growth. Models estimate growth to peak at 26–27°C and stop at <3°C or >32°C (Houde 1974;

Luo & Brandt 1993). Growth occurs primarily during spring and summer and declines during autumn and winter (Luo & Brandt 1993; Wang & Houde 1994; Bassista & Hartman 2005). The majority of growth occurs in larval and juvenile fish and is essentially complete by age 1. In laboratory experiments, food availability significantly affected larval growth (Saksena & Houde 1972; Houde 1977), and stocking density had a smaller effect (Cowan & Houde 1990). In the wild, food along with temperature is the primary determinant of growth because limiting densities likely rarely occur given high predation on Bay Anchovy.

Bay Anchovy experience high growth rates during larval and juvenile stages that slow drastically in older fish. Model simulations estimated growth rates to be 0 mm/day for eggs, 0 mm/day for yolk-sac larvae, 0.7 mm/day for larvae, and 0.092 mm/day for young-of-the-year juveniles and adults (Rose et al. 1999). In the laboratory, growth rates ranged from 0.39 to 0.63 mm/day for larvae (Cowan & Houde 1990). Growth rate might be latitude dependent with faster growth at higher latitudes (Lapolla 2001b), but conclusive data are lacking. From north to south, the average growth rates of wild populations of Bay Anchovy are: 0.7 mm/day (Narragansett Bay, 29- to 84-day-old larvae, Lapolla 2001b), 0.57 mm/day (Great South Bay, 2- to 15-day-old larvae, Castro & Cowen 1991), about 0.52 mm/day (Hudson River Estuary, age of larvae not given, Jordan et al. 2000), 0.40 mm/day (Chesapeake Bay, 15- to 101-day-old larvae, Kimura et al. 2000), 0.48 mm/day (Newport River Estuary, 1- to 48-day-old larvae, Fives et al. 1986), and 0.43–0.56 mm/day (Biscayne Bay, 3- to 23-day-old larvae, Leak & Houde 1987). The averages show a slight latitudinal decrease of growth rate, but the ranges of growth rates overlap greatly among these field studies.

Mortality

The mortality rates for Bay Anchovy are highest during the egg and larval stages, especially during the first 2 days post-spawning. Model simulations estimated that 99% of eggs died before reaching juvenile stages (Rose et al. 1999), and field studies estimated up to 99.2% of eggs died 20-h post-spawn in Hudson Bay (Bassista & Hartman 2005). Mortality rates after the larval stage are stable and comparatively low relative to egg and larval mortality (Castro & Cowen 1991). The life history strategies of the Bay Anchovy, early maturation and high fecundity, offset initially high mortality rates.

Population Ecology

The typical Bay Anchovy population consists primarily of young-of-the-year and age-1 fish; age-2 fish are rare, and age-3+ fish are exceedingly rare. The mean overall sex ratios of Bay Anchovy populations are either a 1M:1F ratio (Lapolla 2001a; Bassista & Hartman 2005) or slightly biased toward females (Vouglitois et al. 1987; Newberger & Houde 1995).

Bay Anchovy can be described as being annual, extremely abundant, and productive. The short life span of this species, usually <1 year, creates an annual turnover of individuals (Newberger & Houde 1995). Year-to-year recruitment fluctuations therefore have a large effect on annual abundance, biomass, and production (MacGregor & Houde 1996). They are the dominant species by abundance and biomass in many surveys and can comprise >90% of fish caught in some places (Reis & Dean 1981). In the northern Gulf of Mexico they are the most abundant species of fish, and in estuaries along the Atlantic and Gulf Coasts, Bay Anchovy have the greatest biomass of any species (Griffith & Bechler 1995 and references therein). Nevertheless, variation in year-to-year abundances of populations is considerable (Derickson & Price 1973; Livingston et al. 1976; Vouglitois et al. 1987). Seasonal abundance for a population can vary in response to temperature and season in northern populations (Fig. 11.10) (Vouglitois et al. 1987) and precipitation in southern populations (Castillo-Rivera et al. 1994). For typical temperate populations, age-1+ fish are most abundant during the spring and early summer, but in the late summer and autumn after peak spawning young-of-the-year become the most abundant. During winter, abundance of young-of-the-year and adults is low in estuaries because of mortality and migration to deeper water (Vouglitois et al. 1987; Wang & Houde 1995). The entire population abundance and biomass peaks during the late summer and early fall when young-of-the-year are most abundant.

Biomass and abundance show similar temporal patterns. Biomass maximizes each year when the late post-larval and juvenile (about 0.3 year) stages of peak-spawned Bay Anchovy occur (Newberger & Houde 1995), minimizes in winter, and remains low and stable in spring and summer. Peak biomass in Chesapeake Bay was 15 g/m^2 during November and lower during spring and summer (3–4 g/m^2, Luo & Brandt 1993). Bay Anchovy biomass can be high; the estimated adult biomass in Chesapeake Bay for June and July 1993 was 23 million kg (Rilling & Houde 1999).

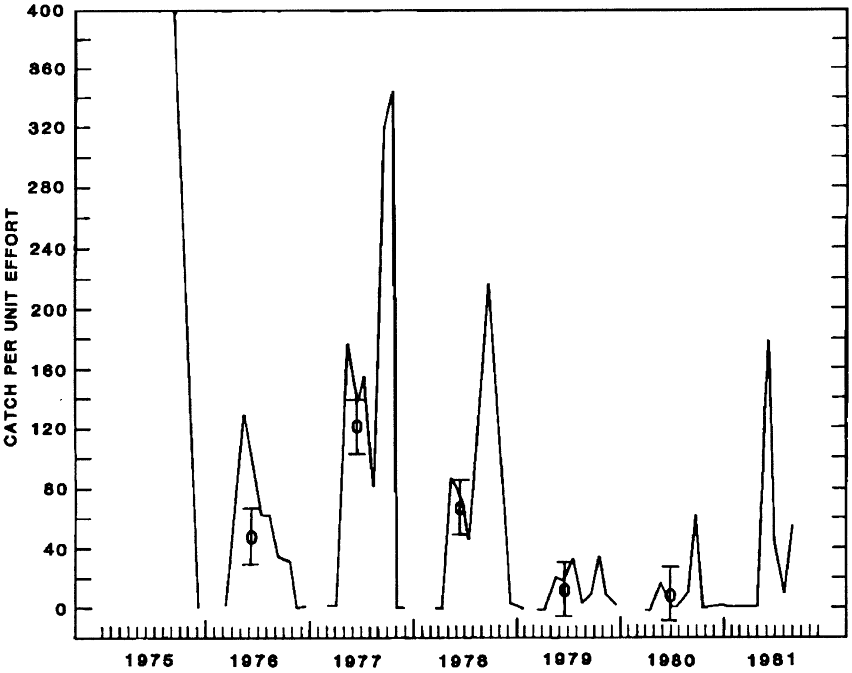


Figure 11.10. Seasonal and annual fluctuations of the Bay Anchovy, *Anchoa mitchilli*, abundance in Barnegat Bay, New Jersey, based on monthly and annual mean trawl catches/unit effort. Open circles indicate annual means, and vertical lines through the means indicate the least significant differences (P = 0.05) (reprinted from Vouglitois et al. 1987 with permission from the American Fisheries Society)

Productivity behaves similarly to abundance and biomass. Productivity peaks during the late summer and autumn, is low during the winter, and increases during the spring and early summer. Production by Bay Anchovy is highest in larval and juvenile young-of-the-year fish, and >80% of young-of-the-year production occurs in the first three months of life (Wang & Houde 1995; Wang et al. 1997). Also, young-of-the-year production can account for >90% of total annual production for an entire population. One estimate of annual production of upper and middle Chesapeake Bay was >211 million kg (Wang & Houde 1995).

Importance as Predators

Bay Anchovy feed on a wide range of prey items (Fig. 11.9), but eat primarily zooplankton. Because Bay Anchovy are usually abundant, they can impact their prey populations. Short-term reductions in zooplankton are correlated with high densities of this species (Johnson et al. 1990), and young-of-the-year alone can consume ≤50% of the zooplankton standing stock during peak biomass (Cowan et al. 1999). During the summer, juvenile Bay Anchovy may consume 60% of their body weight/day (Luo & Brandt 1993), and adult fish consume ≤25% (Hartman et al. 2004). During autumn and winter when prey availability decreases, consumption also sharply decreases for both young-of-the-year and adult fish. Bay Anchovy also can affect the life history patterns of crabs by feeding on their larvae (Morgan 1990). In response, crab larvae can develop defensive morphologies to avoid being eaten or disperse to predator-free areas.

Importance as Prey

This fish serves as a critical trophic link in many food webs due to its ability to transfer so much planktonic energy into available energy for other predators (Johnson et al. 1990; Luo & Brandt 1993; Newberger & Houde 1995; Dorsey et al. 1996; Scharf et al. 2002). Many economically important predatory fishes use Bay Anchovy as their primary forage, especially during times of peak abundances (Morton 1989; Juanes et al. 1993; Hartman & Brandt 1995; Buckel et al. 1999; Scharf et al. 2002). In Chesapeake Bay, Bay Anchovy provided 70% (summer), 90% (autumn), and 60% (spring) of the total energy intake of the truly carnivorous fishes (e.g., *Pomatomus saltatrix*, Bluefish; *Cynoscion regalis*, Weakfish; *Paralichthys dentatus*, Summer Flounder; *Morone saxatilis*, Striped Bass). These predatory fishes consumed 66% (summer), 80% (autumn), 5% (winter), and 54% (spring) of Bay Anchovy secondary production (Baird & Ulanowicz 1989). Bay Anchovy also composed >40% (by weight) of the diet of <100 mm spring-spawned Bluefish in the Hudson River Estuary, New York, and were preyed heavily on by small- and medium-sized Bluefish <120 mm (Juanes et al. 1993).

Bay Anchovy are not strong swimmers, occur in schools, are abundant, and do not grow large enough to avoid being eaten (Scharf et al. 2002), making them easy prey items for many predators (Hildebrand 1963). Some examples of other predatory fishes that feed on Bay Anchovy are *Cynoscion arenarius* (Sand Seatrout), *Cynoscion nebulosus* (Spotted Seatrout), *Lagodon rhomboides* (Pinfish), *Strongylura marina* (Atlantic Needlefish), *Synodus foetens* (Inshore Lizardfish), and *Trachinotus falcatus* (Permit) (Hildebrand 1943; Carr & Adams 1973; Vouglitois et al. 1987). Water birds (Hildebrand 1943; Mettee et al. 1996) and gelatinous predators (Rilling & Houde 1999) also prey on Bay Anchovy. Obviously, any fluctuation in the abundance or production of Bay Anchovy could impact these predators.

Ecological Limitations

Bay Anchovy have few obvious ecological limitations because of their ability to withstand a wide range of environmental conditions in diverse habitats and their high fecundity. Prey availability may play a role in limiting Bay Anchovy production. In laboratory experiments, food concentrations can have significant effects on the survival and growth of Bay Anchovy young-of-the-year (Houde 1977). Bay Anchovy are probably only slightly limited by food availability in the wild and can survive at relatively low food concentrations (Luo & Brandt 1993; Allen et al. 1995). High Bay Anchovy population densities can also have a negative effect on growth because of increased competition for available prey (Wang et al. 1997).

Parasites

Recorded parasites of Bay Anchovy include isopods, copepods, and mussels. Several species of Isopoda in the family Cymothoidae are parasites of Bay Anchovy. *Aegathoa medialis* (Watling et al. 1974), *Aegathoa oculata* (Williams & Williams 1978), and *Nerocila acuminata* (Segal 1987) attach to Bay Anchovy. *Olencira praegustator*, typically thought of as a host-specific parasite of species of menhaden (Clupeidae: *Brevoortia* spp.), attaches to Bay Anchovy in laboratory and natural settings (Watling et al. 1974; Trilles 2007). Parasitic copepods of the genus *Caligus* (Siphonostomatoida: Caligidae) parasitize post-larval Bay Anchovy, attaching to the dorsal surface between the pectoral and dorsal fins. An infection rate of 3.6% occurred (54 of 1,498 post-larval Bay Anchovy) in Calcasieu Estuary, Louisiana (Felley et al. 1987). *Lernaeenicus radiatus* (Siphonostomatoida: Pennellidae) parasitized Bay Anchovy in Florida (Hutton 1964). Bay Anchovy also serve as a host for the glochidia of a freshwater mussel, *Glebula rotundata* (Unionoida: Unionidae) in Louisiana. The glochidia occurred on the gills of Bay Anchovy. Due to the nature of Bay Anchovy, these fish may explain the presence of *G. rotundata* in estuarine habitats even though it is generally found in fresh water (Parker et al. 1984).

CONSERVATION

Anchoa mitchilli is currently stable throughout its range, not currently listed as being threatened or endangered, and not in immediate need of conservation efforts (Warren et al. 2000; Boschung & Mayden 2004). Routine biological monitoring is still advised due to this species' great importance to the estuarine and marine ecosystems as forage for both noncommercial and commercial species.

COMMERCIAL IMPORTANCE

Some species of Engraulidae are important commercially in Old World countries and South America. Those species of Anchovies are canned whole, used in the production of Anchovy paste, and used for bait, and, in some instances, larger species are sold whole at market (Hildebrand 1963). North America does not yet exploit Anchovies commercially because of these species' small sizes and propensity for dying when handled (Morton 1989). Even though Bay Anchovy (and other Anchovy species) are not exploited directly in North America, the species is still incredibly important commercially. Bay Anchovy can be the primary forage fish for commercial and recreational fish species such as the Seatrout, Weakfish, Striped Bass, Summer Flounder, Bluefish, and Mackerels (see ecology section; Hildebrand 1963; Robinette 1983; Newberger & Houde 1995). The abundance and biomass of the species could also serve as an important indicator of environmental conditions in estuaries.

LITERATURE GUIDE

A key to the genera plus a brief summary and distributional map of each extant engraulid species is provided in the FAO Species Catalogue for Engraulididae (= Engraulidae)

(Whitehead et al. 1988). Kells & Carpenter (2011) feature a colored painting of the species. For extinct and fossil species Grande & Nelson (1985) and Grande (1985) are thorough; *Anchoa* spp. fossils specifically are mentioned in Stringer (1992). For phylogenetic relationships in Engraulidae, Lavoué et al. (2009) and Li & Ortí (2007) are good molecular-based sources, and Di Dario (2002, 2009) focuses on morphology. Anchovy morphology is described in detail in several places, including Whitehead et al. (1988), Hildebrand & Schroeder (1928), Hildebrand (1943), and Jones et al. (1978). The eyes of Anchovies are unique in several ways from those of other vertebrates, and Fineran & Nicol (1976, 1977, 1978) provide good figures and summaries. Much of the research done on Bay Anchovy has focused on reproductive biology and life history in specific geographical areas (Vouglitois et al. 1987; Luo & Musick 1991; Zastrow et al. 1991; Bassista & Hartman 2005). Information about egg and larval development is covered in Kuntz (1915), Jones et al. (1978), and Mansueti & Hardy (1967). Baird & Ulanowicz (1989) show how important Bay Anchovy can be within an ecosystem by determining seasonal food webs in Chesapeake Bay. Able & Fahay (2010) provide a good summary of the ecology and biology of Bay Anchovy.

Chapter 12 Cyprinidae: Carps and Minnows

Nicholas J. Gidmark and Andrew M. Simons

The family Cyprinidae (Carps and Minnows) is contained in the Otophysi, a large monophyletic group that includes Characiformes (e.g., African Tetras, Alestiidae; Characins, Characidae); Cypriniformes (e.g., Carps and Minnows, Cyprinidae; Suckers, Catostomidae; and Loaches, Cobitidae); Siluriformes, Catfishes; and Gymnotiformes, American Knifefishes (Fink & Fink 1981; Nelson 2006). All otophysans have a Weberian apparatus that creates an otophysic connection (a connection between the inner ear and gas bladder). The Weberian apparatus is a complex of modified vertebrae, neural arches, ribs, and supraneurals (Fink & Fink 1981) that act as a sound tranducer, transferring vibrations of the gas bladder into mechanical action at the inner ear. This increases the hearing ability of these fishes, particularly at higher frequencies. This Weberian apparatus may represent a key innovation responsible for the incredible success of otophysans, which dominate the fauna of many freshwater environments.

Cyprinids occur in Africa, Asia, Europe, and North America but are absent from Australia and South America. The cyprinids are the largest family of freshwater fishes and may be the largest family of vertebrates with the possible exception of Gobiidae (Gobies). In the family, >2,400 described species are allocated to 220 genera (Nelson 2006). The name Cyprinidae is derived from the Latinized form of the Greek word “kyprinos,” meaning “carp” (Brown 1956). Within cyprinids, North American genera are generally recognized as being contained in the subfamily Leuciscinae together with a number of Asian and European taxa (Mayden et al. 2008).

These fishes are well known to most people and include a huge variety of familiar aquarium and ornamental species such as the Goldfish (*Carassius auratus*), barbs (e.g., Cherry Barb, *Puntius titteya*), and rasboras (e.g., Harlequin Rasbora, *Rasbora heteromorpha*). The Zebra Danio (*Danio rerio*) is a model organism for geneticists and developmental biologists, and the Common Carp (*Cyprinus carpio*) is variously revered as a pet (koi), reared for food, or reviled as an invasive species. Cyprinids, particularly the North American species, represent a tremendous opportunity for biologists in several fields. Their substantial variation in morphology, complex genetic patterns, and impressive range of interesting reproductive behaviors make them a rich group to study. The ease with which cyprinids can be manipulated and maintained in captivity makes this endeavor tractable.

Large gaps exist in our understanding of the evolution and biology of North American cyprinids as will be evident from this chapter. We believe these gaps represent opportunities for biologists in many fields. In that regard, deciding on a taxonomy for North American cyprinids was a difficult task. Older, more familiar classifications (such as those used in many catalogues and field guides) have somewhat understandably not kept pace with contemporary science. The combination of phylogenetic systematics with molecular techniques has rapidly transformed the understanding of the evolutionary history of North American and worldwide cyprinids, and taxonomy should reflect this history. We elected here to use a taxonomy that reflected the most up-to-date evolutionary hypotheses at the time of writing, and as a result, some of the scientific names used in this chapter may be new to some readers. Common names still provide a stable nomenclature, and we used common names consistent with name lists, catalogues, and field guides (e.g., Nelson et al. 2004; Page & Burr 2011; Eshmeyer 2013). Scientific names are less stable than common names because they are hypotheses of evolutionary relationships, but scientific names are more biologically informative. Unfortunately, some species were not included in contemporary studies and at this time cannot be placed in such a classification. These species, all formerly classified in *Notropis*, are referred to here as *"Notropis."* We hope this taxonomy will highlight interesting relationships, emphasize gaps in knowledge, and thus stimulate and help prioritize research across biological disciplines on these fascinating fishes.

DIVERSITY AND DISTRIBUTION

The extant native North American cyprinid fauna contains 57 genera and at least 300 species (Table 12.1). The classification we use is based on the most recent studies of North American cyprinid systematics (see phylogenetic relationships section) and largely relies on the classification of Mayden et al. (2006). In the following subsections, the diversity and distribution of the 8 largest genera of North American cyprinids—those with ≥9 described species—are summarized, and those likely harboring cryptic species are noted. In some cases, the most wide-ranging and range-restricted species in the genus are highlighted as are general characteristics of species in a genus. Genera are presented in order by size. The remaining 49 genera are not detailed separately, and we refer the reader to the distribution maps (Figs. 12.1–12.55) and life history tables for all genera (Tables 12.2–12.5).

Genus *Notropis*

The largest genus, *Notropis*, contains 56 species (including those placed in *"Notropis"*; Table 12.1) that are distributed widely across North America (Fig. 12.1). The genus

Table 12.1. Generic classification of North American cyprinid species. This table includes undescribed species that have long been recognized by ichthyologists. It does not include undescribed species proposed in recent phylogeographic studies that have not been substantiated by additional data.

Genus	Size	Included Extant Species
Notropis	21	*amabilis*, *amoenus*, *ariommus*, *atherinoides*, *buchanani*, *cahabae*, *girardi*, *jemezanus*, *leuciodus*, *micropteryx oxyrhynchus*, *ozarcanus*, *percobromus*, *peripallidus*, *rubellus*, *spectrunculus*, *stilbius*, *suttkusi*, *volucellus*, *wickliffi*, *N.* sp. (Sawfin Shiner)
"Notropis"	36	*aguirrepequenoi*, *albizonatus*, *alborus*, *amecae*, *ammophilus*, *anogenus*, *atrocaudalis*, *aulidion*, *bifrenatus*, *boops*, *braytoni*, *chihuahua*, *dorsalis*, *greenei*, *heterolepis*, *longirostris*, *maculatus*, *mekistocholas*, *melanostomus*, *nazas*, *nubilus*, *orca*, *ortenburgeri*, *oxyrhynchus*, *photogenis*, *rafinesquei*, *rupestris*, *sabinae*, *saladonis*, *scabriceps*, *scepticus*, *semperasper*, *simus*, *telescopus*, *tropicus*, *uranoscopus*
Cyprinella	30	*analostana*, *alvarezdelvillari*, *bocagrande*, *caerulea*, *callisema*, *callistia*, *callitaenia*, *camura*, *chloristia*, *forlornensis*, *formosa*, *galactura*, *garmani*, *gibbsi*, *labrosa*, *leedsi*, *lepida*, *lutrensis*, *nivea*, *panarcys*, *proserpina*, *pyrrhomelas*, *rutila*, *spiloptera*, *trichroistia*, *venusta*, *whipplei*, *xaenura*, *xanthicara*, *zanema*
Alburnops	20	*asperifrons*, *baileyi*, *bairdi*, *blennius*, *buccula*, *candidus*, *chalybaeus*, *chiliticus*, *chlorocephalus*, *chrosomus*, *edwardraneyi*, *hypsilepis*, *lutipinnis*, *petersoni*, *potteri*, *rubricroceus*, *shumardi*, *texanus*, *xaenocephalus*, *A.* sp. (Piedmont Shiner)
Gila	18	*atraria*, *brevicauda*, *conspersa*, *coricacea*, *cypha*, *ditaenia*, *elegans*, *eremica*, *intermedia*, *minacae*, *modesta*, *nigrescens*, *orcutti*, *pandora*, *pulchra*, *purpurea*, *robusta*, *seminuda*
Lythrurus	11	*alegnotus*, *ardens*, *atrapiculus*, *bellus*, *fasciolaris*, *fumeus*, *lirus*, *matutinus*, *roseipinnis*, *snelsoni*, *umbratilus*
Macrhybopsis	11	*aestivalis*, *australis*, *hyostoma*, *gelida*, *marconis*, *meeki*, *storeriana*, *tetranema*, *M.* sp. (Gulf Chub), *M.* sp. (Coosa Chub), *M.* sp. (Pallid Chub)
Pteronotropis	10	*euryzonus*, *grandipinnis*, *harperi*, *hubbsi*, *hypselopterus*, *metallicus*, *merlini*, *signipinnis*, *stonei*, *welaka* (but see phylogenetic relationships section)
Luxilus	9	*albeolus*, *cardinalis*, *cerasinus*, *chrysocephalus*, *coccogenis*, *cornutus*, *pilsbryi*, *zonatus*, *zonistius*
Algansea	7	*lacustris*, *aphanea*, *avia*, *barbata*, *monticola*, *popoche*, *tincella*
Chrosomus	7	*cumberlandensis*, *eos*, *erythrogaster*, *neogaeus*, *oreas*, *saylori*, *tennesseensis*
Hybognathus	7	*amarus*, *argyritus*, *hankinsoni*, *hayi*, *nuchalis*, *placitus*, *regius*
Hybopsis	7	*amblops*, *amnis*, *hypsinotus*, *lineapunctata*, *rubifrons*, *winchelli*, *H.* sp. (Coastal Chub)

(continued)

Table 12.1, continued

Genus	Size	Included Extant Species
Nocomis	7	*asper*, *biguttatus*, *effusus*, *leptocephalus*, *micropogon*, *platyrhynchus*, *raneyi*
Rhinichthys	7	*atratulus*, *cataractae*, *evermanni*, *falcatus*, *obtusus*, *osculus*, *umatilla*
Dionda	6	*argentosa*, *diaboli*, *episcopa*, *melanops*, *nigrotaeniata*, *serena*
Tampichthys	6	*catostomops*, *dichroma*, *erimyzonops*, *ipni*, *mandibularis*, *rasconis*
Campostoma	6	*anomalum*, *oligolepis*, *ornatum*, *pauciradii*, *pullum*, *spadiceum*
Erimystax	5	*cahni*, *dissimilis*, *harryi*, *insignis*, *x-punctatus*
Lepidomeda	5	*albivallis*, *alicae*, *copei*, *mollispinis*, *vittata*
Phenacobius	5	*catostomus*, *crassilabrum*, *mirabilis*, *teretulus*, *uranops*
Miniellus	4	*heterodon*, *procne*, *stramineus*, *topeka*
Pimephales	4	*notatus*, *promelas*, *tenellus*, *vigilax*
Ptychocheilus	4	*grandis*, *lucius*, *oregonensis*, *umpquae*
Semotilus	4	*atromaculatus*, *corporalis*, *lumbee*, *thoreauianus*
Graodus	3	*boucardi*, *cumingii*, *moralesi*
Hudsonius	3	*altipinnis*, *cummingsae*, *hudsonius*
Siphateles	3	*alvordensis*, *bicolor*, *boraxobius*
Agosia	2	*chrysogaster*, *A.* sp. (Pupo mexicano, Mexican Longfin Dace)
Aztecula	2	*calientis*, *sallei*
Clinostomus	2	*elongatus*, *funduloides*
Ericymba	2	*buccata*, *amplamala*
Exoglossum	2	*laurae*, *maxilinguae*
Oregonichthys	2	*crameri*, *kalawatseti*
Richardsonius	2	*balteatus*, *egregius*
Acrocheilus	1	*alutaceus*
Codoma	1	*ornata*
Couesius	1	*plumbeus*
Eremichthys	1	*acros*
Erimonax	1	*monachus*
Hemitremia	1	*flammea*
Hesperoleucas	1	*symmetricus*
Iotichthys	1	*phlegethontis*
Klamathella	1	*coerulea*
Lavinia	1	*exilicauda*
Margariscus	1	*margarita*
Meda	1	*fulgida*
Mylocheilus	1	*caurinus*
Mylopharodon	1	*conocephalus*
Notemigonus	1	*crysoleucas*
Opsopoeodus	1	*emiliae*
Orthodon	1	*macrolepidotus*
Plagopterus	1	*argentissimus*
Platygobio	1	*gracilis*
Pogonichthys	1	*macrolepidotus*
Relictus	1	*solitarius*
Tiaroga	1	*cobitis*
Yuriria	1	*alta*

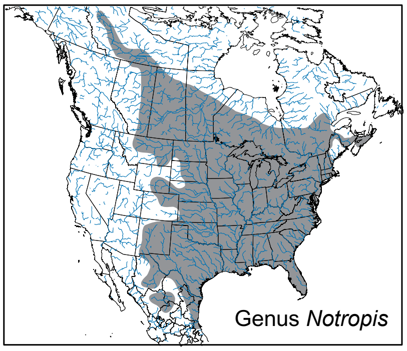

Genus *Notropis*

Figure 12.1. Geographic range of *Notropis*.

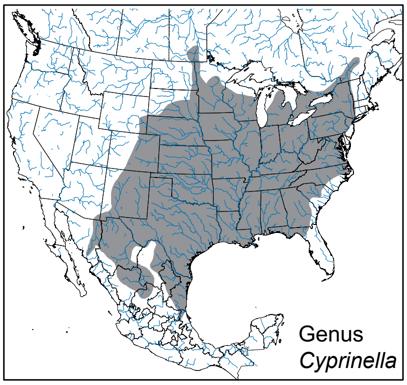

Genus *Cyprinella*

Figure 12.2. Geographic range of *Cyprinella*.

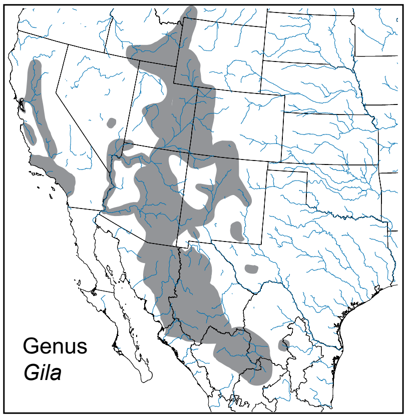


Figure 12.3. Geographic range of *Gila*.

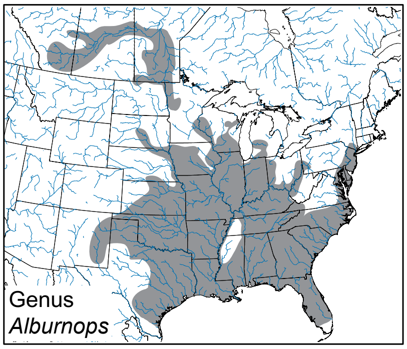

Genus *Alburnops*

Figure 12.4. Geographic range of *Alburnops*.

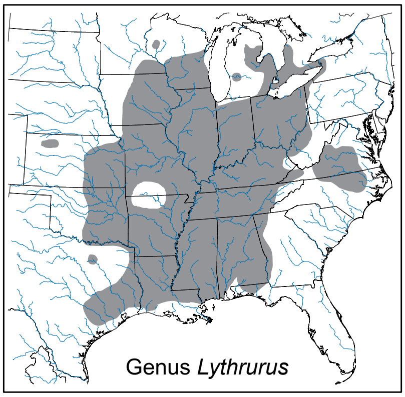

Genus *Lythrurus*

Figure 12.5. Geographic range of *Lythrurus*.

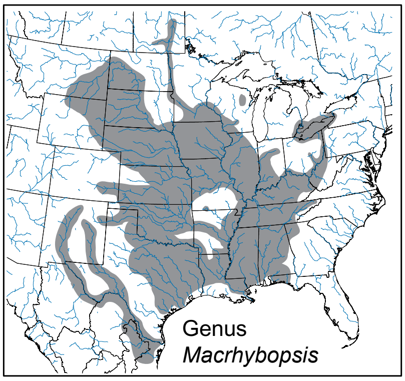

Genus *Macrhybopsis*

Figure 12.6. Geographic range of *Macrhybopsis*.

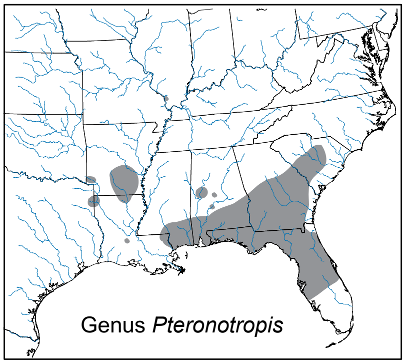

Genus *Pteronotropis*

Figure 12.7. Geographic range of *Pteronotropis*.

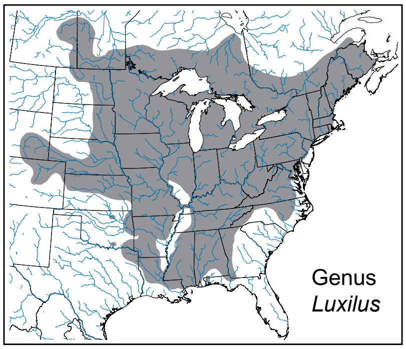

Genus *Luxilus*

Figure 12.8. Geographic range of *Luxilus*.

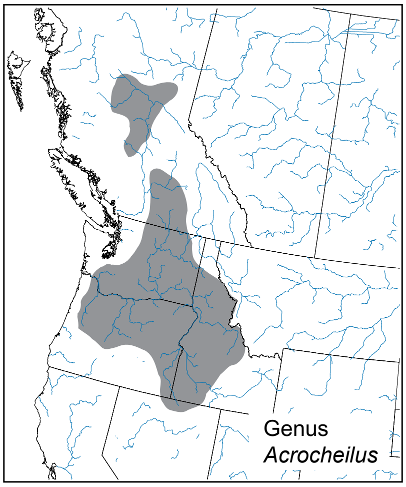

Genus *Acrocheilus*

Figure 12.9. Geographic range of *Acrocheilus*.

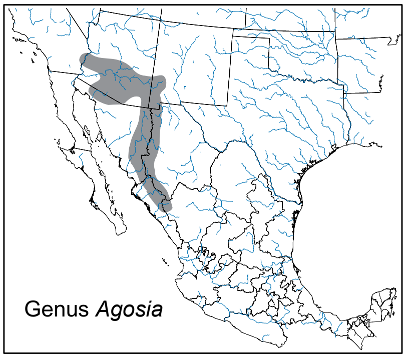

Genus *Agosia*

Figure 12.10. Geographic range of *Agosia*.

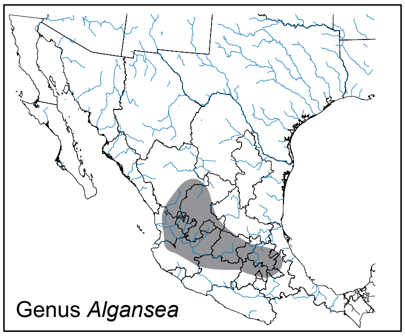

Genus *Algansea*

Figure 12.11. Geographic range of *Algansea*.

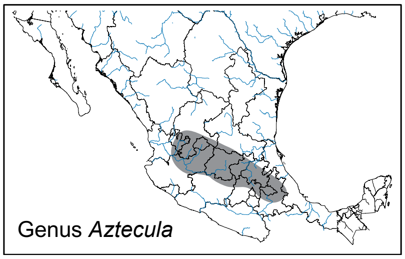

Genus *Aztecula*

Figure 12.12. Geographic range of *Aztecula*.

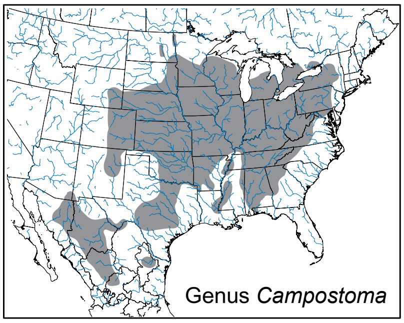

Genus *Campostoma*

Figure 12.13. Geographic range of *Campostoma*.

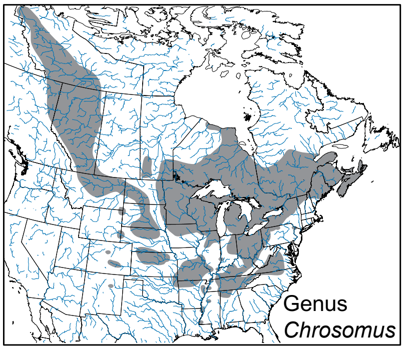

Genus *Chrosomus*

Figure 12.14. Geographic range of *Chrosomus*.

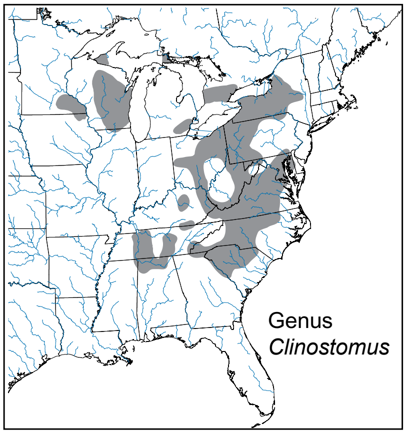

Genus *Clinostomus*

Figure 12.15. Geographic range of *Clinostomus*.

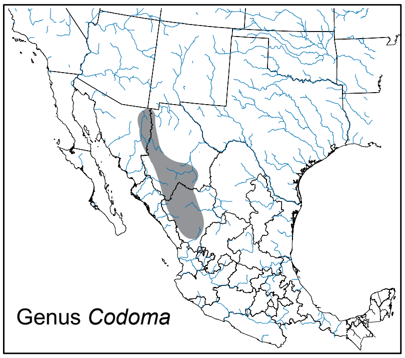

Genus *Codoma*

Figure 12.16. Geographic range of *Codoma*.

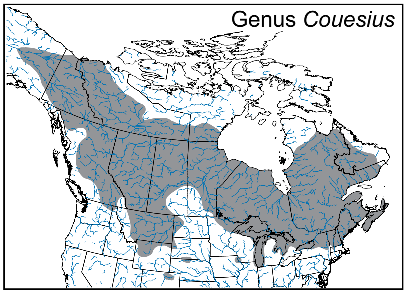

Genus *Couesius*

Figure 12.17. Geographic range of *Couesius*.

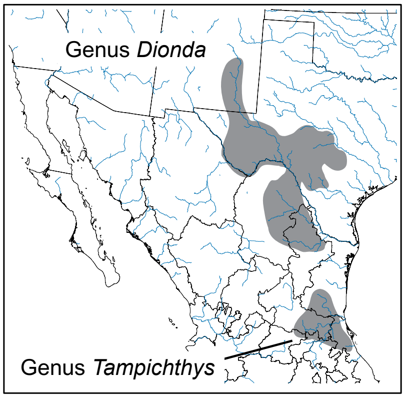

Genus *Dionda*
Genus *Tampichthys*

Figure 12.18. Geographic range of *Dionda* and *Tampichthys*.

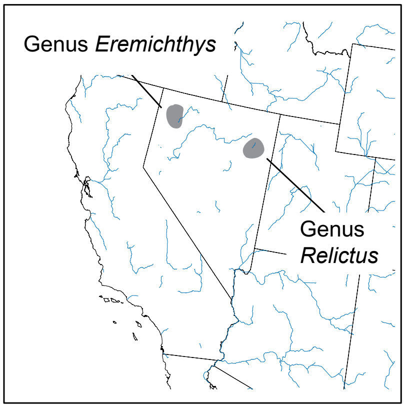

Genus *Eremichthys*
Genus *Relictus*

Figure 12.19. Geographic range of *Eremichthys* and *Relictus*.

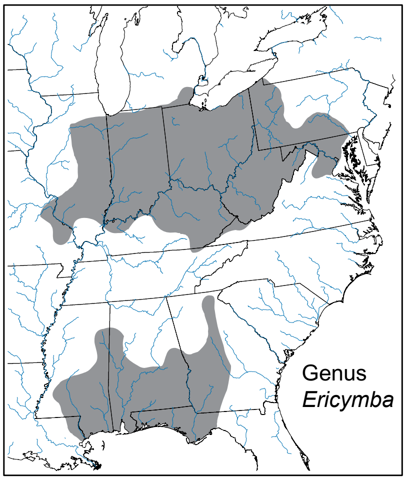

Genus *Ericymba*

Figure 12.20. Geographic range of *Ericymba*.

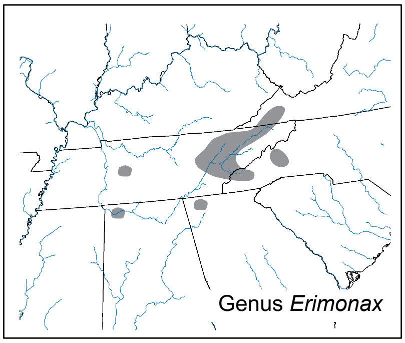

Genus *Erimonax*

Figure 12.21. Geographic range of *Erimonax*.

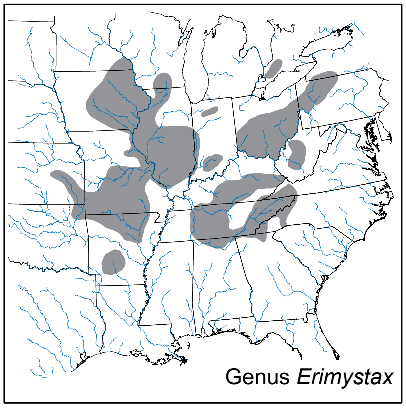

Genus *Erimystax*

Figure 12.22. Geographic range of *Erimystax*.

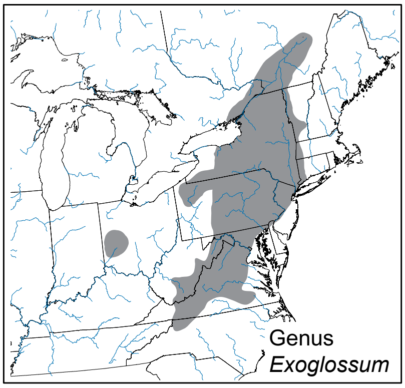

Genus *Exoglossum*

Figure 12.23. Geographic range of *Exoglossum*.

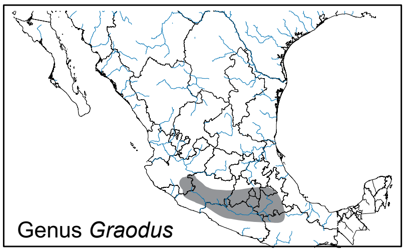

Genus *Graodus*

Figure 12.24. Geographic range of *Graodus*.

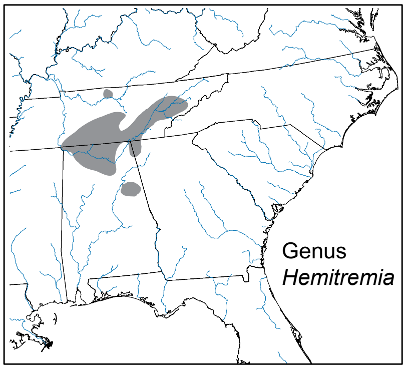

Genus
Hemitremia

Figure 12.25. Geographic range of *Hemitremia*.

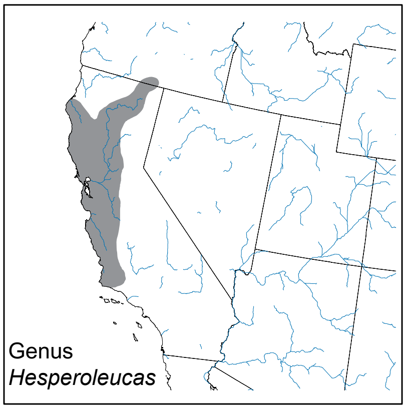

Genus
Hesperoleucas

Figure 12.26. Geographic range of *Hesperoleucas*.

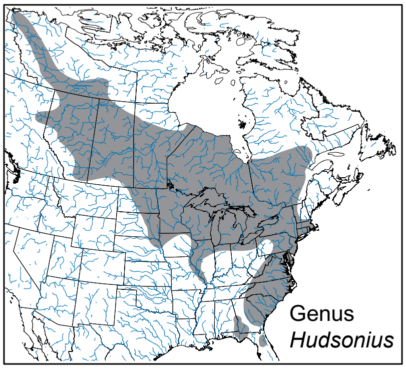

Genus
Hudsonius

Figure 12.27. Geographic range of *Hudsonius*.

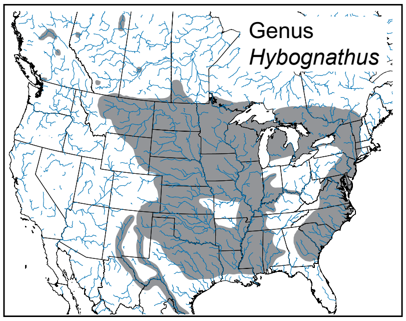

Genus
Hybognathus

Figure 12.28. Geographic range of *Hybognathus*.

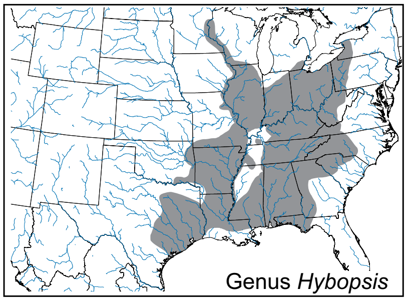

Genus *Hybopsis*

Figure 12.29. Geographic range of *Hybopsis*.

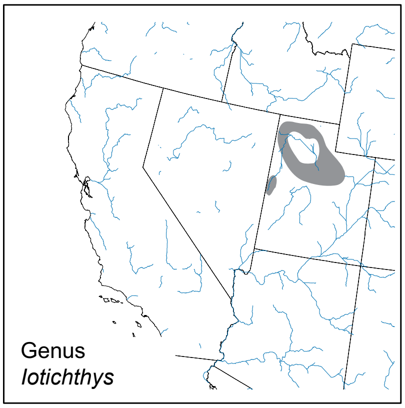

Genus
Iotichthys

Figure 12.30. Geographic range of *Iotichthys*.

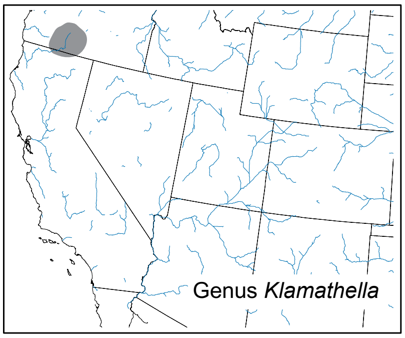

Genus *Klamathella*

Figure 12.31. Geographic range of *Klamathella*.

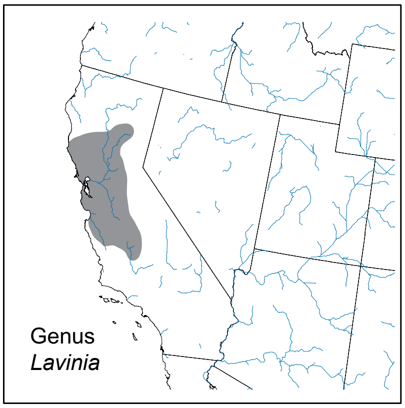

Genus
Lavinia

Figure 12.32. Geographic range of *Lavinia*.

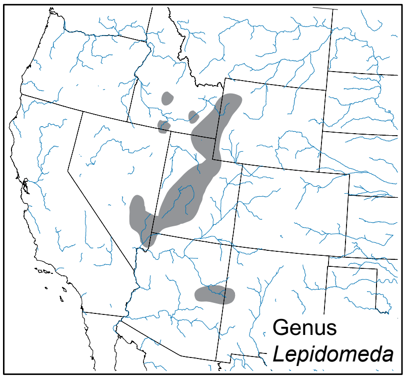

Genus
Lepidomeda

Figure 12.33. Geographic range of *Lepidomeda*.

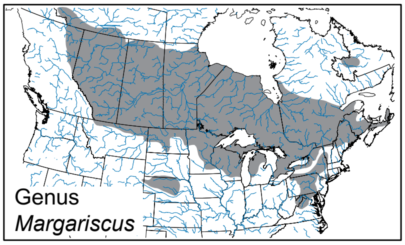

Genus
Margariscus

Figure 12.34. Geographic range of *Margariscus*.

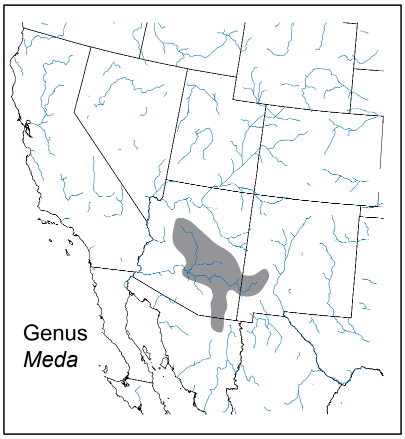


Figure 12.35. Geographic range of *Meda*.

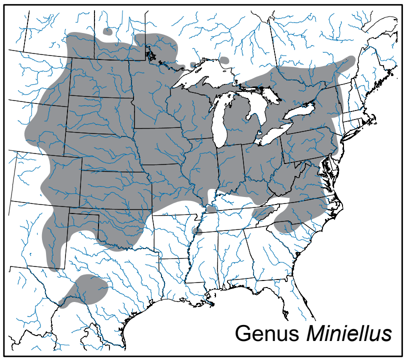

Genus *Miniellus*

Figure 12.36. Geographic range of *Miniellus*.

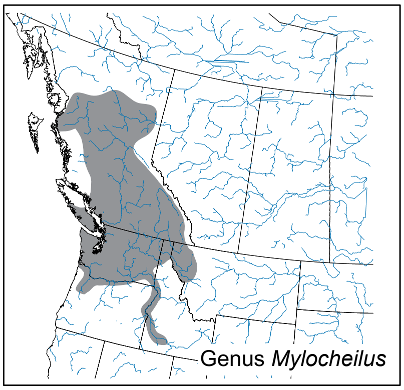

Genus *Mylocheilus*

Figure 12.37. Geographic range of *Mylocheilus*.

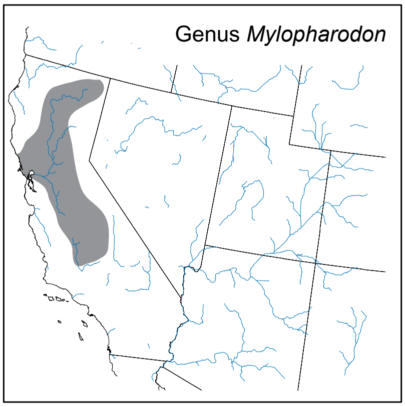

Genus *Mylopharodon*

Figure 12.38. Geographic range of *Mylopharodon*.

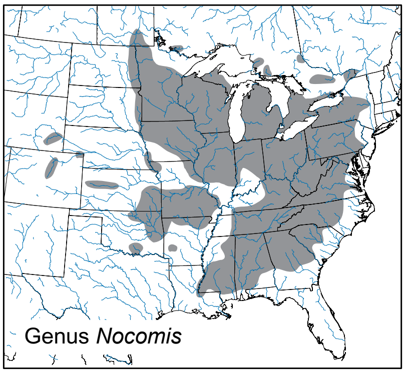

Genus *Nocomis*

Figure 12.39. Geographic range of *Nocomis*.

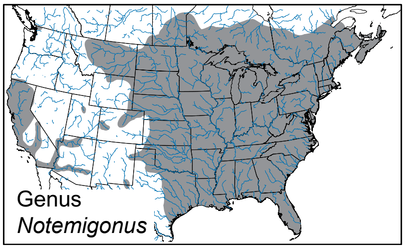

Genus
Notemigonus

Figure 12.40. Geographic range of *Notemigonus*.

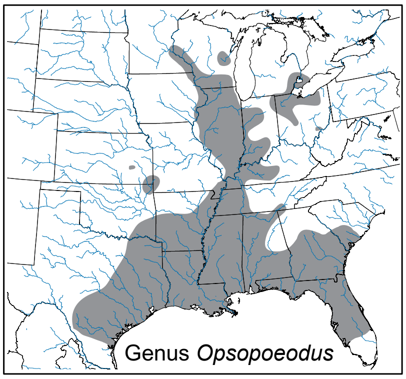

Genus Opsopoeodus

Figure 12.41. Geographic range of *Opsopoeodus*.

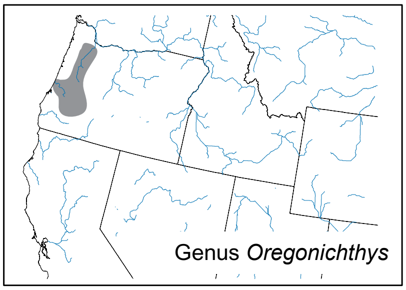

Genus Oregonichthys

Figure 12.42. Geographic range of *Oregonichthys*.

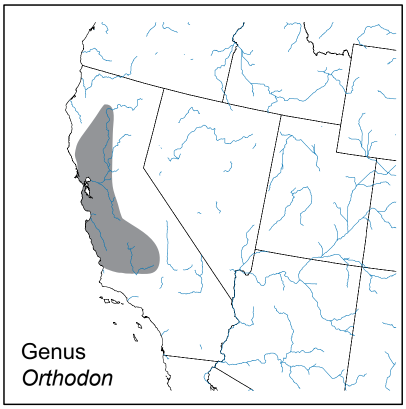

Genus
Orthodon

Figure 12.43. Geographic range of *Orthodon*.

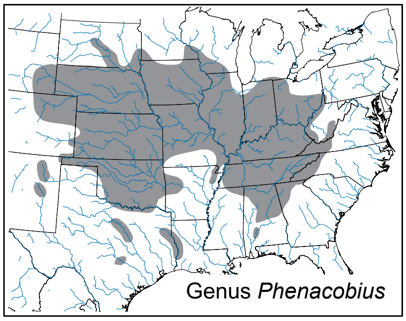

Genus Phenacobius

Figure 12.44. Geographic range of *Phenacobius*.

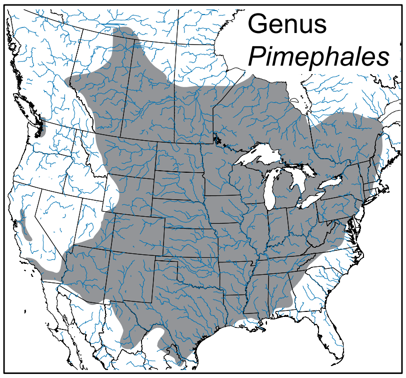

Genus
Pimephales

Figure 12.45. Geographic range of *Pimephales*.

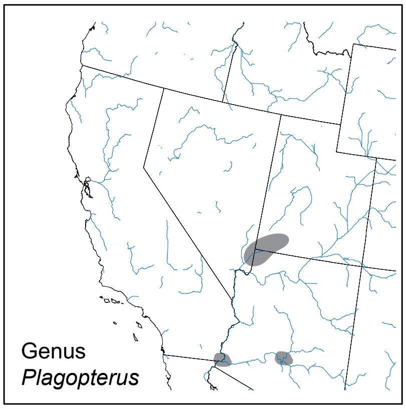

Genus
Plagopterus

Figure 12.46. Geographic range of *Plagopterus*.

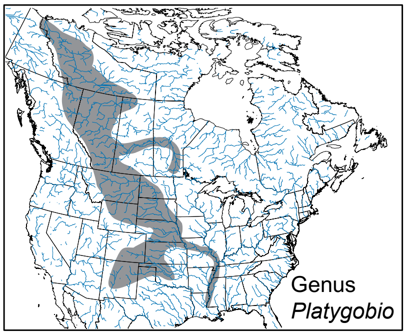

Genus
Platygobio

Figure 12.47. Geographic range of *Platygobio*.

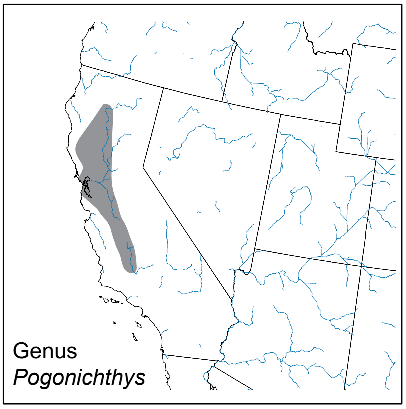

Genus
Pogonichthys

Figure 12.48. Geographic range of *Pogonichthys*.

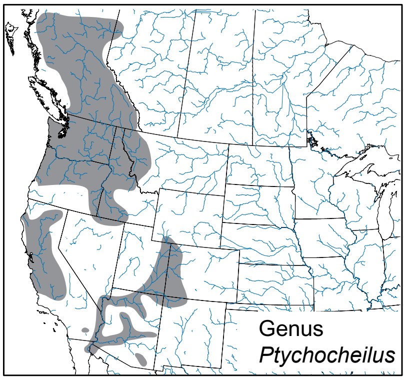

Genus
Ptychocheilus

Figure 12.49. Geographic range of *Ptychocheilus*.

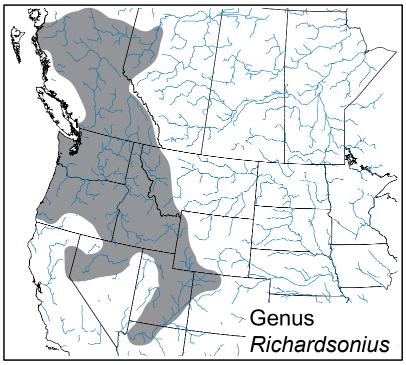

Genus
Richardsonius

Figure 12.50. Geographic range of *Richardsonius*.

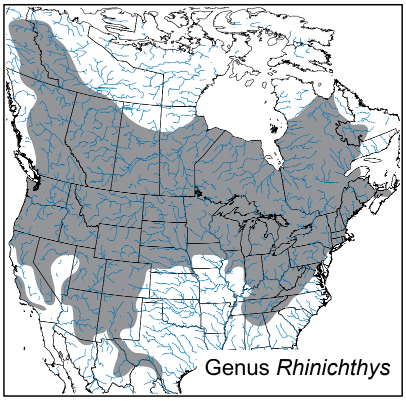

Genus *Rhinichthys*

Figure 12.51. Geographic range of *Rhinichthys*.

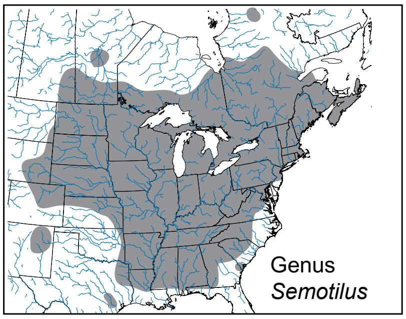

Genus
Semotilus

Figure 12.52. Geographic range of *Semotilus*.

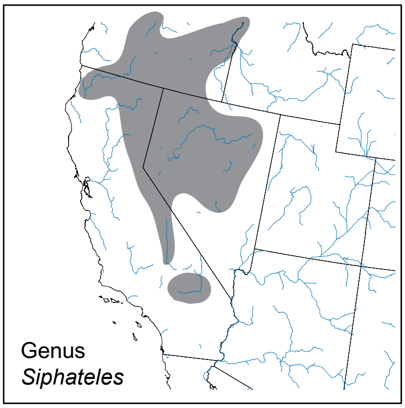

Genus
Siphateles

Figure 12.53. Geographic range of *Siphateles*.

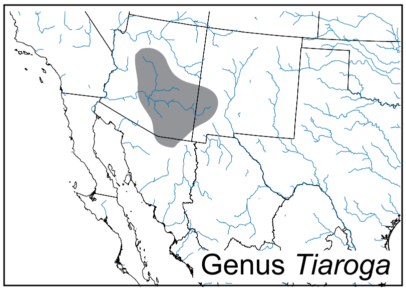

Genus *Tiaroga*

Figure 12.54. Geographic range of *Tiaroga*.

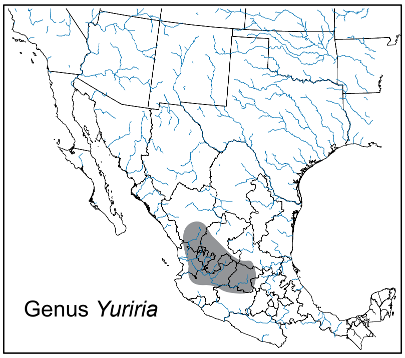

Genus *Yuriria*

Figure 12.55. Geographic range of *Yuriria*.

Table 12.2. Life history data for type species of *Couesius*, *Hemitremia*, *Lepidomeda*, *Margariscus*, *Meda*, *Plagopterus*, *Semotilus*, and *Notemigonus*. Parenthetical numbers refer to [1]Barber et al. 1970; [2]Becker 1983; [3]Blinn et al. 1998; [4]Boschung & Mayden 2004; [5]Bryan 1999; [6]Buynak & Mohr 1980b; [7]Etnier & Starnes 1993; [8]Fava & Tsai 1974; [9]Fuiman et al. 1983; [10]Greger & Deacon 1987; [11]Jelks et al. 2008; [12]Jenkins & Burkhead, 1994; [13]McPhail 2007; [14]Minckley & Carufel 1967; [15]Moshenko & Gee 1973; [16]Roberge et al. 2002; [17]Schemske 1974; [18]Schwartz 1981; [19]Scott & Crossman 1973; [20]Sigler & Sigler 1996; [21]Sublette et al. 1990; [22]Trautman 1981.

Life History Traits	***Couesius plumbeus***	***Hemitremia flammea***	***Lepidomeda vittata***	***Margariscus margarita***	***Meda fulgida***	***Plagopterus argentissimus***	***Semotilus atromaculatus***	***Notemigonus crysoleucas***
Clade	Creek Chub + plagopterin	Creek Chub + plagopterin	Creek Chub + plagopterin	Creek Chub + plagopterin	Creek Chub + plagopterin	Creek Chub + plagopterin	Creek Chub + plagopterin	Leuciscinae
Number of extant species	One	One	Five	One	One	One	Four	One
1 or 2 degree freshwater	1	1	1	1	1	1	1	1, brackish (≤27 ppt; 18)
Maximum size recorded in length	227 mm TL (19)	78 mm SL (7)	150 mm TL (5)	158 mm TL (16)	75 mm TL (21)	89 mm TL (20)	303 mm TL (2)	267 mm TL (22)
Maximum age	5 years (16)	2–3 years (4)	4 years (3)	4 years (16)	3 years (1)	3 years (20)	7 years (12)	9 years (12)
Age and size at first reproduction	3–4 years; size not given (16)	1 year; 33 mm SL (4)	1 year (3); 64 mm TL (3)	2 years; size not given (19)	1 year (21); 40 mm SL (1)	Unknown	1 year but usually 2 years; size not given (12)	1–3 years; 50–70 mm SL (12)
Iteroparous or semelparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous
Fecundity estimates (ovarian counts)	500–10,000 (13, 19)	2,000 (4)	650–5,000 (14)	912–4,240 (2, 8)	100–800 (21)	Unknown	1,115–7,539 (15, 17)	200,000 (12)
Egg deposition sites	Demersal, non-adhesive (13, 16)	Gravel (4)	Gravel (5)	Sand-gravel (12)	Demersal over sand and gravel (1)	Sand (20)	Pit-ridge nests (12)	Adhesive on vegetation, gravel, Sunfish nests (12, 19)
Clutch size	N/A	N/A	N/A	N/A	N/A	N/A	50 (7)	N/A

Range of nesting and spawning dates and temperatures	May–August depending on latitude (16, 19); 10°C (13, 16)	December–May; 11–17°C (4)	Late May–early June (5); 16°C (3)	12–18°C (13, 19)	April–late May (1)	April–May; 14.4°C (20)	March–May or June; 12–18°C (12)	Mid-April–early August; 21–26°C (12)
Habitat of spawning sites; average water depth	Shallow water (16)	Spring-fed streams (4)	Shallow streams; 3.8 cm (3)	Organic material, sand, gravel; <0.6 m (2, 16)	Sand or gravel substrate; <15 cm (21)	Flowing water; 25 mm deep (20)	Streams with sand or gravel substrate (19)	Pools and slow-moving streams (12, 19)
Incubation period	5–10 days (13)	3–4 days	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Mean size at hatching	6 mm TL (13)	Unknown	6–7 mm TL (3)	Unknown	Unknown	Unknown	6.8–7.5 mm TL (9)	4.0–4.3 mm TL (6)
Parental care	None (16)	None (4)	None (5)	None (2)	None (21)	None (20)	None	None
Major dietary items	Insects, algae, freshwater shrimp, small fishes (16)	Dipteran larvae, other small invertebrates (4, 7)	Aquatic and terrestrial invertebrates (5)	Invertebrates, plankton, filamentous algae (16)	Aquatic and terrestrial insects (21)	Aquatic insect larvae (10, 20)	Fishes, crayfish, mollusks, insects (12)	Microcrustaceans, terrestrial and aquatic insects (12)
General year-round habitat	Lakes, streams, rivers (16)	Springs and spring-fed streams (7)	Stream pools and glides (5)	Variable; bogs, streams, lakes	Clear, low- to moderate-gradient streams (21)	Streams (20)	Creeks 2–7 m wide (12)	Lakes, slow-moving streams, swamps (12, 19)
Migratory or diadromous	≤1.6 km for spawning (2)	None	None	None	None	None	None	None
Imperilment status; number of species	None	Vulnerable; one (11)	Endangered; three Threatened; one Vulnerable, one (11)	None	Endangered; one (11)	Endangered; one (11)	None	None

Table 12.3A. Life history data for type species of *Campostoma*, *Clinostomus*, *Erimystax*, *Exoglossum*, *Iotichthys*, *Macrhybopsis*, *Mylocheilus*, and *Nocomis*. Parenthetical numbers refer to [1]Becker 1983; [2]Billman et al. 2010; [3]Bottrell et al. 1964; [4]Buynak & Mohr 1980a; [5]Cooper 1980; [6]COSEWIC 2008; [7]Crawford 1979; [8]Etnier & Starnes 1993; [9]Evans-White et al. 2001; [10]Jelks et al. 2008; [11]Jenkins & Burkhead 1994; [12]McPhail 2007; [13]Pappantoniou et al. 1983; [14]Platania & Altenbach 1988; [15]Roberge et al. 2002; [16]Scott & Crossman 1973; [17]Sigler & Sigler 1996; [18]Sublette et al. 1990; [19]Van Duzer 1939.

Life History Traits	***Campostoma anomalum***	***Clinostomus funduloides***	***Erimystax dissimilis***	***Exoglossum maxillinguae***	***Iotichthys phlegethontis***	***Macrhybopsis aestivalis***	***Mylocheilus caurinus***	***Nocomis biguttatus***
Clade	Non-shiner OPM	Non-shiner OPM	Non-shiner OPM	Non-shiner OPM	Non-shiner OPM	Non-shiner OPM	Non-shiner OPM	Non-shiner OPM
Number of extant species	Four	Two	Five	Two	One	Eight	One	Seven
1 or 2 degree freshwater	1	1	1	1	1	1	2	1
Maximum size recorded in length	287 mm TL (11)	115 mm TL (8)	140 mm TL (8)	140 mm TL (16)	76 mm TL (17)	60 mm SL (18)	310 mm FL (16)	225 mm TL (1)
Maximum age	6 years (11)	4 years (11)	3 years (11)	5 years (11)	4 years (17)	1.5 years (18)	19 years (12)	4 years (16)
Age and size at first reproduction	1–2 years; 110 mm SL (1, 11)	1 year; 53 mm TL (11)	1 year; size not given (11)	Age not given; 75–100 mm TL (?) (19)	1 year; 25 mm TL (17)	1 year, based on *M. hyostoma;* size not given (1)	2 years; size not given (12)	2 years (1); 64 mm TL (1)
Iteroparous or semelparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous
Fecundity estimates (ovarian counts)	563–623 (1)	121–997 (11)	400 (11)	153–744 (13)	300–2,700 (17)	559, based on *M. hyostoma*, (1)	10,000–20,000 (12)	460–952 (1, 16)
Egg deposition sites	Shallow pits in gravel (11)	Nest associate with *Nocomis*, *Semotilus* (8)	Not observed	Gravel mound 0.2–0.5 m wide (11)	Adhesive eggs on vegetation (7)	Semi-buoyant eggs, during flood events (14)	Adhesive, demersal eggs deposited on gravel (12)	Stone and pebble nest (16)
Clutch size	150–4,800 (11)	N/A	Unknown	Unknown	N/A	N/A	N/A	Unknown

Range of nesting and spawning dates and temperatures	April–June; 10.8–26.8°C (1, 11)	April–June; 12.7–25.2°C (11)	April–May; 15°C (8)	May–July; 16.1–21.5°C (11)	April–July; at least 15.6°C (17)	Late spring to autumn; above 21°C (18)	May–June; 10–15°C (15)	May–July (1); 18.3°C or warmer (1)
Habitat of spawning sites; average water depth	Small streams; 15–20 cm deep (1)	Shallow streams; as little as 5 cm (8)	Not observed	Streams, slow runs, pools, and back waters (11)	Shallow water on spring margins (2)	Large rivers	Stony rubble substrate, lakes (15); 5 cm deep (16)	Clear, slow, gravelly streams (16); >1.0 m deep (1)
Incubation period	69–71 h at 21.1°C (1)	Unknown	Unknown	Unknown	2.1 days at 22.2°C (2)	24–48 h, based on *M. tetranema* (3)	6 days at 18°C (12)	Unknown
Mean size at hatching	5.7 mm TL (4)	Unknown	Unknown	5.5–5.7 mm TL (4)	Unknown	Unknown	7 mm TL (12)	5.7–6.5 mm TL, based on *N. micropogon* (5)
Parental care	None	None	None, based on *E. x-punctatus* (6)	Eggs covered with pebbles	None	None	None	Males guard nests (1)
Major dietary items	Detritus, algae, diatoms, occasional insects (1, 11, but see 9).	Aquatic and terrestrial invertebrates (11)	Benthic insect larvae, other benthic invertebrates (11)	Caddisfly larvae and other aquatic invertebrates (11)	Macroinvertebrates, algae, diatoms (17)	Aquatic insects, based on *M. hyostoma* (1)	Aquatic and terrestrial insects (16)	Snails, aquatic insects, annelids, crayfish, small fish (16)
General year-round habitat	Clear streams of moderate to high gradient (11)	Creeks and streams (11)	Large streams and rivers (11)	Moderate-gradient streams and rivers (11)	Rivers, streams, springs, swamps (2)	Turbid streams	Lakes, rivers (15)	Clear, low-gradient streams and rivers (16)
Migratory or diadromous	None	None	None	None	None	None	Unknown	None
Imperilment status; number of species	Vulnerable; one (10)	Vulnerable; two (10)	Endangered; one Vulnerable; one (10)	None	Endangered; one (10)	Endangered; one Threatened; one Vulnerable; five (10)	None	None

Table 12.3B. Life history data for type species of *Oregonichthys*, *Phenacobius*, *Platygobio*, *Pogonichthys*, *Rhinichthys*, *Richardsonius*, and *Tiaroga*. Parenthetical numbers refer to [1]Becker 1983; [2]Cooper 1980; [3]Jelks et al. 2008; [4]Jenkins & Burkhead 1994; [5]Kristensen 1980; [6]Markle et al. 1991; [7]McPhail 2007; [8]McPhail & Lindsey 1970; [9]Moyle 2002; [10]Roberge et al. 2002; [11]Scheerer & McDonald 2003; [12]Scott & Crossman 1973; [13]Sublette et al. 1990; [14]Vives & Minckley 1990.

Life History Traits	***Oregonichthys crameri***	***Phenacobius teretulus***	***Platygobio gracilis***	***Pogonichthys macrolepidotus***	***Rhinichthys cataractae***	***Richardsonius balteatus***	***Tiaroga cobitis***
Clade	OPM (Non-shiner)	OPM (Non-shiner)	OPM (Non-shiner)	OPM (Non-shiner)	OPM (Non-shiner)	OPM (Non-shiner)	OPM (Non-shiner)
Number of extant species	Two	Five	One	One	Seven	Two	One
1 or 2 degree freshwater	1	1	1	2	1	1	1
Maximum size recorded in length	57.5 mm SL (6)	110 mm TL (4)	370 mm TL (5)	400 mm SL (9)	178 mm TL (1)	180 mm TL (12)	60 mm SL (13)
Maximum age	9 years (11)	2 years (4)	14 years (7)	>8 years (9)	5 years (1)	7 years (10)	3 years (13)
Age and size at first reproduction	2 years (34); 40 mm SL (11)	1 year; 50 mm (4)	5 years; 85 mm SL (10)	2 years (9); 170 mm SL (9)	2 years; size not given (4)	3 years; size not given (10)	2 years; size not given (13)
Iteroparous or semelparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous
Fecundity estimates (ovarian counts)	147–671 (6)	Unknown	7,000–15,000 (7)	>100,000 (9)	1,400–2,800 (1)	829–3,602 (12)	144–1,200 (13)
Egg deposition sites	Aquatic vegetation (6)	Large gravel (4)	Not observed	Adhesive eggs deposited on vegetation and debris (9)	Small depressions in sand or gravel (4)	Adhesive demersal eggs on gravel, vegetation (12)	Adhesive eggs in cavities under flattened cobble (13, 14)
Clutch size	Unknown	N/A	Unknown	N/A	200–1,200 (8)	Unknown	9–260 (13, 14)
Range of nesting and spawning dates and temperatures	April–July (6); 11–15°C (11)	Late April–early June; 19.4°C (4)	June–August; 18–25°C (13)	February–July; 14–19°C (9)	June–early July (10); 11–23°C (4)	May–August; 14.5–18°C (10)	Late March–early June; 16–21°C (13). September (23°C) also reported (14)

Habitat of spawning sites; average water depth	Vegetated areas of still or slow water (6)	Stream runs; 0.3–1 m deep (4)	Unknown	Flooded vegetation (9)	Shallow areas of fast, flowing water (4)	Riffles; 0.1 m (10)	Flowing water; 6–21 cm deep (13)
Incubation period	Unknown	Unknown	Unknown	3–7 days (9)	7–10 days at 15.6°C (8)	3 days at 21°C, 15 days at 12°C (12)	6 days at 21°C (13)
Mean size at hatching	Unknown	Unknown	Unknown	Unknown	4.5–5.9 mm TL (2)	5.3 mm TL (12)	Unknown
Parental care	None	None	None	None	Eggs defended by at least one parent (10)	None	Males defend eggs from predators (14)
Major dietary items	Small invertebrates (6)	Benthic insect larvae and other benthic inverts (4)	Insects (10), small fishes, and the occasional young rodent (8)	Detritus, benthic invertebrates (9)	Aquatic insects (10)	Aquatic invertebrates (10), fish eggs, and small fishes (12)	Benthic aquatic insects (13)
General year-round habitat	Still to slow-flowing water (6)	Clear, moderate-gradient streams (4)	Muddy, turbid, large rivers (10)	Sloughs, lakes, rivers (9)	Fast-flowing streams, lakeshores (10)	Streams and lakes (7, 12)	High- to moderate-gradient large streams (13)
Migratory or diadromous	None	None	Small streams to spawn (10)	Upstream to spawn (9)	None	Migrate to streams to spawn (12)	None
Imperilment status; number of species	Endangered; one Vulnerable; two (3)	None	None	Vulnerable; one (3)	Vulnerable; two Various populations and subspecies of *R. cataractae* and *R. osculus* considered Endangered, Threatened, and Vulnerable (3)	None	Threatened; one (3)

Table 12.4A. Life history data for type species of *Agosia*, *Alburnops*, *Algansea*, *Aztecula*, *Codoma*, *Cyprinella*, *Dionda*, and *Ericymba*. Parenthetical numbers refer to [1]Barbour & Miller 1978; [2]Becker 1983; [3]Cross 1967; [4]Etnier & Starnes 1993; [5]Fuiman et al. 1983; [6]Gale 1986; [7]Gibson & Fries 2005; [8]Jelks et al. 2008; [9]Jenkins & Burkhead 1994; [10]Miller et al. 2005; [11]Minckley & Barber 1971; [12]Minckley & Vives 1990; [13]Phillips et al. 2009; [14]Sublette et al. 1990; [15]Trautman 1981; [16]Vives 1993; [17]Wayne 1979; [18]Wayne & Whiteside 1985.

Life History Traits	***Agosia chrysogaster***	***Alburnops blennius***	***Algansea tincella***	***Aztecula sallaei***	***Codoma ornata***	***Cyprinella lutrensis***	***Dionda episcopa***	***Ericymba buccata***
Clade	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)
Number of extant species	Two	Twenty	Seven	Two	One	Thirty	Six	Two
1 or 2 degree freshwater	1	1	1	1	1	1	1	1
Maximum size recorded in length	65 mm SL (14)	132 mm TL (2)	175 mm SL (1)	88 mm SL (10)	58 mm SL (10)	90 mm TL (4)	64 mm SL (14)	97 mm TL (15)
Maximum age	3 years (14)	4 years (2)	Unknown	Unknown	Unknown	3 years (4)	Unknown	4 (9)
Age and size at first reproduction	1 year; size not given (14)	Males, 1 year, 46–64 mm TL; females, 2 years, 70–84 mm TL (2)	Unknown	Unknown	Unknown	2 years (2); 30 mm SL (4)	Presumably age 0–1; 25 mm SL (7)	1 (9)
Iteroparous or semelparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous
Fecundity estimates (ovarian counts)	Unknown	1,895–2,840 (2)	Unknown	Unknown	Unknown	485–684 (2)	2–584, based on *D. nigrotaeniata* (17, 18)	150–1,350 (9)
Egg deposition sites	Saucer-shaped depressions in sand (11)	Over sand and gravel bars (15)	Unknown	Unknown	Adhesive eggs deposited in crevices, under, or between rocks (10, 12)	Adhesive eggs deposited along margins of Sunfish nests, over gravel, or in crevices (2, 3, 16)	Non-adhesive demersal eggs on gravel, based on *D. diaboli* (13, 17, 18)	Sand and gravel (9)

Clutch size	Unknown	N/A	Unknown	Unknown	85–115 (12)	585 (6)	N/A	N/A
Range of nesting and spawning dates and temperatures	Unknown	June–August (2)	May–July (10)	February–May (10)	March–October	May–August, depending on location (2); 15.6–29.4°C (3)	Spring months; >17–18°C (14)	March–May 10–20°C (9)
Habitat of spawning sites; average water depth	Sandy substrate and slight current; 5–20 cm deep (11)	Large rivers (2)	Unknown	Unknown	Clear, flowing pools; between 2.5 and 15 cm deep (12)	Highly variable	Springs (14)	Unknown
Incubation period	4 days at >24°C (11)	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Mean size at hatching	Unknown	Unknown	Unknown	Unknown	Unknown	4–5 mm TL (5)	7 mm TL, based on *D. diaboli* (7)	Unknown
Parental care	None (11)	None	Unknown	Unknown	Males defend eggs (12)	None	None	Unknown
Major dietary items	Detritus, zooplankton, aquatic insects, filamentous algae (14)	Aquatic insects (2)	Unknown	Unknown	Unknown	Plant material, aquatic insect larvae, microinvertebrates (2)	Algae, diatoms (14)	Small, benthic invertebrates (9)
General year-round habitat	Small, clear streams (11)	Large rivers in water 1–3 m deep (2)	Small streams to large lakes (1)	Spring-fed ponds, lakes, streams (10)	Pools and riffles of clear streams and rivers (10)	Turbid and silty streams, rivers, and lakes (2)	Vegetated low-gradient rivers and streams (14)	Creeks and rivers (9)
Migratory or diadromous	None	None	None	Unknown	None	None	None	None
Imperilment status; number of species	Vulnerable; one (8)	Vulnerable; two Threatened; one (8)	Endangered; four Vulnerable; two (8)	Vulnerable; two (8)	Vulnerable; one (8)	Endangered; seven Threatened; two Vulnerable; three (8)	Endangered; four (8)	None

Table 12.4B. Life history data for type species of *Erimonax*, *Graodus*, *Hudsonius*, *Hybognathus*, *Hybopsis*, *Luxilus*, *Lythrurus*, and *Miniellus*. Parenthetical numbers refer to [1]Becker 1983; [2]Contreras-MacBeath & Rivas 2007; [3]Cross 1967; [4]Etnier & Starnes 1993; [5]Hunter & Hasler 1965; [6]Jelks et al. 2008; [7]Jenkins & Burkhead 1994; [8]Miller et al. 2005; [9]Scott & Crossman 1973; [10]Trautman 1981.

Life History Traits	***Erimonax monachus***	***Graodus boucardi***	***Hudsonius hudsonius***	***Hybognathus nuchalis***	***Hybopsis amblops***	***Luxilus chrysocephalus***	***Lythrurus umbratilis***	***Miniellus procne***
Clade	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)
Number of extant species	One	Three	Three	Seven	Seven	Nine	Eleven	Four
1 or 2 degree freshwater	1	1	1	1	1	1	1	1
Maximum size recorded in length	92 mm SL (7)	66 mm SL (8)	147 mm TL (10)	152 mm TL (10)	99 mm TL (10)	240 mm TL (10)	67.4 mm SL (1)	65 mm SL (7)
Maximum age	3 years (7)	Unknown	5 years (7)	3 years (1)	Unknown	6 years (7)	3 years (1)	3 years (7)
Age and size at first reproduction	2 years; 53 mm SL (7)	Unknown	1–4 years (1); 55 mm SL (7)	2 years (1); 65 mm TL (1)	1 year (7); 58 mm TL (10)	2 years; 60 mm SL (7)	1 year; 28–32 mm SL (4)	2 years (7); 39 mm SL (7)
Iteroparous or semelparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous
Fecundity estimates (ovarian counts)	157–791 (7)	Unknown	100–8,898 (7)	2,054–3,105 (1)	Unknown	900–1,150 (7)	219–887 (1, 4)	Unknown
Egg deposition sites	Adhesive eggs in rock crevices or between rocks (7)	Rocky substrate (2)	Sand, gravel, algae (1)	Non-adhesive eggs deposited on vegetation, *H. regius* (4)	Unknown	*Nocomis* or *Campostoma* nests; males may excavate shallow pits (7, 9)	Gravel and sand in stream or green Sunfish nests (5, 9)	Sand, Sunfish and cyprinid nests (7)
Clutch size	Unknown	N/A	N/A	N/A	Unknown	50 (9)	Unknown	Unknown

Range of nesting and spawning dates and temperatures	Mid-May–mid-August; 26.1–27.2°C (7)	January–April (8)	April–early September (7)	April–July (1)	Late spring and early summer (4)	May–June; 16–26.7°C (7)	June–August (1, 9); 21°C or higher (3)	May–July (7); 25.6°C (7)
Habitat of spawning sites; average water depth	Moderate current in shallow stream runs (7)	Shallow water during low-flow conditions (2)	Over sand and algae in shallow riffles; lakes up to 4.6 m (1, 7, 9)	Unknown	Unknown	Streams over gravel substrate (7, 9)	Green Sunfish nests; 4–35 cm (1)	In moderate current (7)
Incubation period	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Mean size at hatching	Unknown	Unknown	Unknown	Unknown	Unknown	6.9 mm TL (1)	Unknown	Unknown
Parental care	Unknown	None (2)	None	None	Unknown	None	None	None
Major dietary items	Benthic aquatic insect larvae, 99% immature midge and blackfly larvae (7)	Small, benthic, aquatic insects (2)	Larval insects, algae, microcrustaceans, mollusks, small fishes (7)	Algae, blue-green algae, diatoms (1)	Microcrustaceans and midge larvae (7)	Aquatic and terrestrial insects	Aquatic and terrestrial insects, filamentous algae (1)	Aquatic invertebrates, filamentous algae (7)
General year-round habitat	Warm, clear, medium-size streams of moderate gradient (7)	Shallow streams with rocky substrate (2)	Large lakes and rivers (1)	Silty creeks (4) and medium to large rivers in clear waters (1)	Clear creeks, streams, and rivers (7)	Creeks, streams, and rivers	Weedy or turbid pools of low-gradient streams (1, 9)	Pools of large creeks and rivers (7)
Migratory or diadromous	None	Unknown	None	None	None	None	None	Unknown
Imperilment status; number of species	Threatened; one (6)	Threatened; two (6)	None	Endangered; one Vulnerable; two (6)	Vulnerable; two (6)	None	Vulnerable; one (6)	Endangered; one (6)

Table 12.4C. Life history data for type species of *Notropis*, *Opsopoeodus*, *Pimephales*, *Pteronotropis*, *Tampichthys*, and *Yuriria*. Parenthetical numbers refer to [1]Ankley et al. 2001; [2]Becker 1983; [3]Boschung & Mayden 2004; [4]Etnier & Starnes 1993; [5]Jelks et al. 2008; [6]Jenkins & Burkhead 1994; [7]Markus 1934; [8]Mayden & Simons 2002; [9]Miller et al. 2005; [10]Page & Johnston 1990a; [11]Roberge et al. 2002; [12]Scott & Crossman 1973.

Life History Traits	***Notropis atherinoides***	***Opsopoeodus emiliae***	***Pimephales promelas***	***Pteronotropis hypselopterus***	***Tampichthys rasconis***	***Yuriria alta***
Clade	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)	Shiner (OPM)
Number of extant species	Fifty-six	One	Four	Ten	Six	One
1 or 2 degree freshwater	1	1	1	1	1	1
Maximum size recorded in length	97 mm TL (2)	66 mm TL (4)	102 mm TL (6)	58 mm SL (3)	53 mm SL (9)	200 mm SL (9)
Maximum age	4 years (6)	2 years (2)	3 years (11)	Unknown	Unknown	Unknown
Age and size at first reproduction	2 years; 46 mm SL (6)	1 year; 48 mm TL (2)	<1 year (7); 40 mm TL (6)	Unknown	Unknown	Unknown
Iteroparous or semelparous	Iteroparous	Iteroparous	Iteroparous; but 80% spawning mortality (7)	Iteroparous	Iteroparous	Iteroparous
Fecundity estimates (ovarian counts)	888–5,443 (6)	200–340 (2)	4,000–5,000 (7)	Unknown	Unknown	Unknown
Egg deposition sites	Gravel	Undersides of flat objects (4, 10)	Cavities, underside of rocks, logs, plants (7)	Unknown	Crevices between rocks, based on *T. dichroma* (8)	Unknown
Clutch size	N/A	30–120/clutch (10)	8,000 in 1 month (1)	Unknown	Unknown	Unknown
Range of nesting and spawning dates and temperatures	July–late August (11); 20–23°C (6)	March–September (2)	May–August; 15.6–32.0°C (6, 12)	Unknown	March–May (9)	March–June (9)

Habitat of spawning sites; average water depth	Midwater; 2–6 m over clean substrate (11)	Unknown	Nest in water up to 1 m deep (12)	Unknown	Near small spring upwellings, based on *T. dichroma* (8)	Unknown
Incubation period	24–32 h (12)	142 h at 21°C, 105 h at 25°C, 90 h at 27°C (10)	4.5–6 days (12)	Unknown	Unknown	Unknown
Mean size at hatching	4.0 mm TL (12)	5–5.5 mm TL (10)	5 mm TL (12)	Unknown	Unknown	Unknown
Parental care	None	Male defends eggs and nest (10)	Male guards and cleans eggs	Unknown	Male defends eggs, based on *T. dichroma* (8)	Unknown
Major dietary items	Terrestrial and aquatic insects, microcrustaceans and other plankton (6)	Chironomid larvae, microcrustaceans, algae (2)	Aquatic insects, algae; detritus; zooplankton (12)	Unknown	Unknown	Unknown
General year-round habitat	Large, open lakes and rivers (12)	Slow-moving water with vegetation (12)	Still, muddy waters in ponds and small lakes (11)	Small to medium streams (3)	Large, slow-moving streams (9)	Streams with moderate to strong current in depths of 1–3 m (9)
Migratory or diadromous	None	None	None	None	Unknown	Unknown
Imperilment status; number of species	Possibly Extinct; three Endangered; seven Threatened; six Vulnerable; seven (5)	None	Vulnerable; one (5)	Vulnerable; five (5)	Endangered; three (5)	None

Table 12.5A. Life history data for type species of *Acrocheilus*, *Chrosomus*, *Eremichthys*, *Gila*, *Hesperoleucas*, and *Klamathella*. Parenthetical numbers refer to [1]Becker 1983; [2]Brouder et al. 2000; [3]Cross 1967; [4]Etnier & Starnes 1993; [5]Jelks et al. 2008; [6]La Rivers 1962; [7]McPhail 2007; [8]Moyle 2002; [9]Roberge et al. 2002; [10]Scoppettone 1988; [11]Scott & Crossman 1973; [12]Sigler & Sigler 1996; [13]Sublette et al. 1990; [14]Vinyard 1997; [15]Wydoski & Whitney 2003.

Life History Traits	***Acrocheilus alutaceus***	***Chrosomus erythrogaster***	***Eremichthys acros***	***Gila robusta***	***Hesperoleucas symmetricus***	***Klamathella coerulea***
Clade	Western	Western	Western	Western	Western	Western
Number of extant species	One	Seven	One	Eighteen	One (but see 8)	One
1 or 2 degree freshwater	1	1	1	1	1	1
Maximum size recorded in length	225 mm FL (11)	76 mm TL (1)	63.5 mm SL (6)	500 mm SL (13)	120 mm SL (8)	380 mm SL (8)
Maximum age	8 years (9)	3 years (1)	Unknown	7 years (2)	6 years (8)	17 years (10)
Age and size at first reproduction	3–4 years; size not given (9)	1 year; >50 mm TL (1)	Unknown	2 years; size not given (13)	2 years; 45 mm SL (8)	Probably 2–4+ years; 120 mm SL (8)
Iteroparous or semelparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous
Fecundity estimates (ovarian counts)	6,200 (15)	230–862 (1)	Unknown	600–45,125 (13)	250–2,000 (7)	Unknown
Egg deposition sites	Demersal, adhesive eggs on gravel, cobble, boulders (7, 15)	Gravel substrate, *Nocomis* and *Semotilus* nests (1, 4)	Unknown	Adhesive eggs on gravel or rocks (13)	Adhesive eggs deposited in rock crevices (8)	Adhesive eggs deposited on shallow gravel and rock (8)
Clutch size	N/A	N/A	Unknown	N/A	N/A	N/A
Range of nesting and spawning dates and temperatures	Late May–July; 13–18°C (9, 15)	March–July, depending on location (1, 3)	Unknown	June–July when temperatures reach 18.3°C (12)	March–July when temperatures reach 16°C (8)	May–August; 15–18°C (8)
Habitat of spawning sites; average water depth	Streams and lakes (7)	Streams with gravel or pebbles (1)	Unknown	Streams in water; < 9 m deep (12)	Shallow areas of streams (8)	Lakes and rivers; 0.3–0.5 m (8)
Incubation period	16 days at 12°C, 6 days at 18°C (7)	Unknown	Unknown	Unknown	2–3 days (8)	Unknown
Mean size at hatching	8 mm TL (7)	Unknown	Unknown	Unknown	Unknown	Unknown
Parental care	None	None	Unknown	None	None	None
Major dietary items	Diatoms, algae (11)	Algae, diatoms (1)	Algae and invertebrates (14)	Aquatic insects, macroinvertebrates, and fishes (2)	Filamentous algae, aquatic insects, and crustaceans (8)	Aquatic and terrestrial insects (8)
General year-round habitat	Large streams, lakes (7)	Small, clear streams (1)	Hot springs, between 30.6 and 33.9°C (6)	Pools and rapids of medium to large rivers (13)	Small streams and rivers (8)	Small streams, rivers, and lakes (8)
Migratory or diadromous	None	None	None	None	None	None
Imperiled status; number of species	None	Endangered; one Threatened; one Vulnerable; one (5)	Threatened; one (5)	Endangered; seven Threatened; four Vulnerable; four (5)	Vulnerable; one (5)	None

Table 12.5B. Life history data for type species of *Lavinia*, *Mylopharodon*, *Orthodon*, *Ptychocheilus*, *Relictus*, and *Siphateles*. Parenthetical numbers refer to [1]Hankins 1995; [2]Hubbs et al. 1974; [3]Jelks et al. 2008; [4]McPhail 2007; [5]Moyle 2002; [6]Roberge et al. 2002; [7]Scoppettone 1988; [8]Scott & Crossman 1973.

Life History Traits	***Lavinia exilicauda***	***Mylopharodon conocephalus***	***Orthodon macrolepidotus***	***Ptychocheilus oregonensis***	***Relictus solitarius***	***Siphateles bicolor***
Clade	Western	Western	Western	Western	Western	Western
Number of extant species	One	One	One	Four	One	Three
1 or 2 degree freshwater	1	1	1	1	1	1
Maximum size recorded in length	350 mm SL (5)	600 mm SL (5)	500 mm FL (5)	>400 mm FL (4); >1.8 m in *P. lucius* (5)	99 mm SL (2)	420 mm SL (5)
Maximum age	6 years (5)	10 years (5)	>5 years (5)	20 years (6)	Unknown	32 years (7)
Age and size at first reproduction	1 year (5); 49 mm SL (5)	Unknown	2 years (5); 170 mm (5)	4 years; 30 cm (6)	Unknown	2–7 years (5)
Iteroparous or semelparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous	Iteroparous
Fecundity estimates (ovarian counts)	3,000–63,000 (5)	7,000–24,000 (5)	14,700–346,500 (5)	5,000–95,000 (4)	Unknown	11,200–25,000 (5)
Egg deposition sites	Non-adhesive, demersal eggs deposited over gravel (5)	Not observed	Adhesive eggs deposited on vegetation (5)	Adhesive, demersal eggs on gravel and cobble (4, 8)	Aquatic vegetation (2)	Vegetation, algae-covered substrate, sand (5)
Clutch size	N/A	Unknown	N/A	N/A	N/A	N/A
Range of nesting and spawning dates and temperatures	14–26°C (5)	Unknown	March–July; 12–14°C (5)	May–July; 12–18°C (6)	June–September (2)	13–17°C (5)
Habitat of spawning sites; average water depth	Riffles of streams with gravel substrate (5)	Presumed spawning individuals observed in stream riffles (5)	Shallow areas with aquatic plants (5)	Streams, lakeshore (6)	Springs	Vegetation, algae-covered substrate (5); < 1.5 m (5)
Incubation period	3–7 days at 15–22°C (5)	Unknown	Unknown	6 days at 18°C (4)	Unknown	3–6 days (5)
Mean size at hatching	Unknown	Unknown	Unknown	8 mm TL (4)	Unknown	Unknown
Parental care	None	Unknown	None	None	Unknown	None
Major dietary items	Algae, zooplankton, aquatic and terrestrial insects (5)	Benthic invertebrates, aquatic plants, zooplankton (5)	Phytoplankton and zooplankton (5)	Crayfish, fish (6)	Insects (1)	Detritus, plant fragments, zooplankton, macroinvertebrates (5)
General year-round habitat	Low-gradient creeks, slow-moving rivers, lakes (5)	Large streams and rivers (5)	Slow-moving, turbid rivers and lakes (5)	Near shore areas of lakes and large rivers (6)	Clear springs (2)	Springs, slow-moving streams, rivers, and lakes (5)
Migratory or diadromous	To streams to spawn (5)	To streams to spawn (5)	None	Upstream to spawn in tributary rivers (6)	None	None
Imperiled status; number of species	Vulnerable; one (3)	None	None	Endangered; one (3)	Vulnerable; one (3)	Endangered; one Threatened; one Various subspecies and populations considered Endangered, Threatened, and Vulnerable (3)

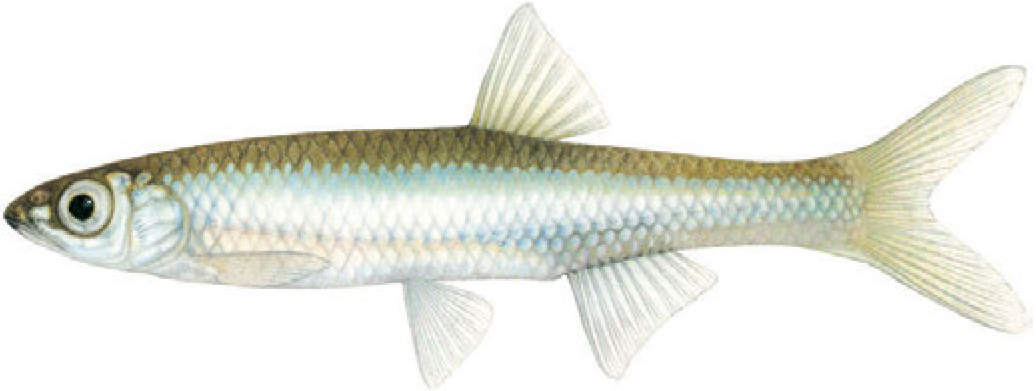


Plate 12.1. Emerald Shiner, *Notropis atherinoides*

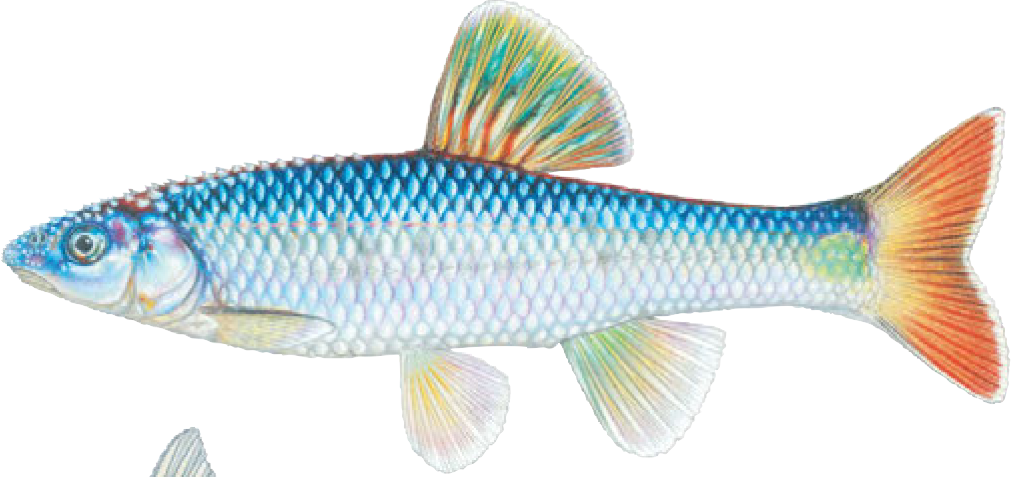


Plate 12.2. Alabama Shiner, *Cyprinella callistia*

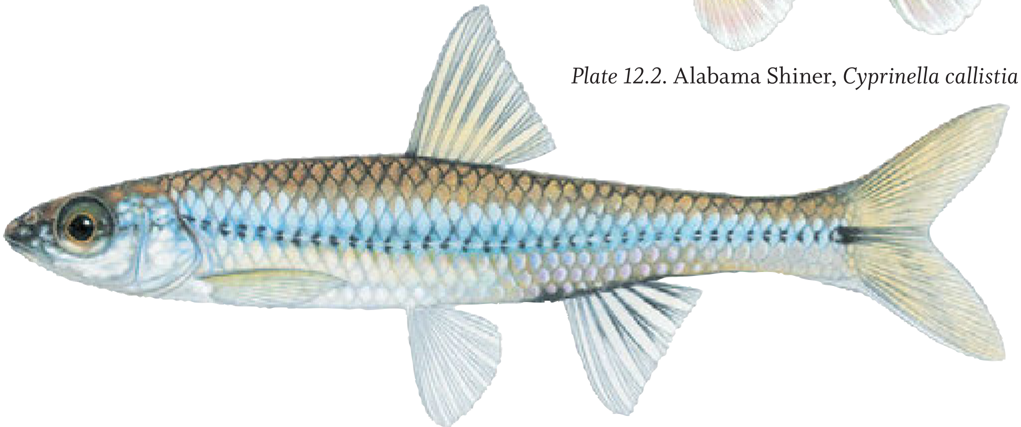


Plate 12.3. Weed Shiner, *Alburnops texanus*

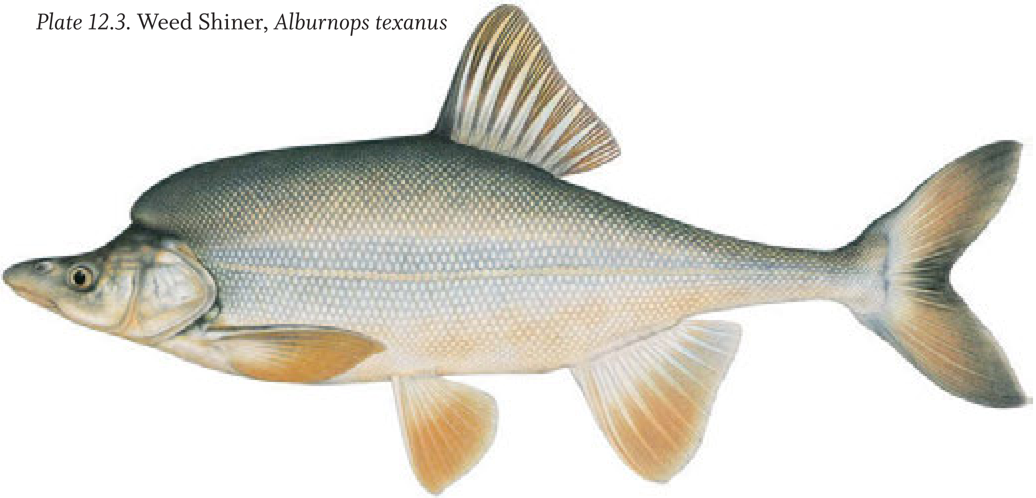


Plate 12.4. Humpback Chub, *Gila cypha*

Notropis is a taxonomic repository for small, silvery fishes of unknown relationship and thus is polyphyletic. This genus may ultimately be reduced to many fewer species once phylogenetic relationships of the shiners are refined. Although absent from Pacific Ocean drainages and the northern Canadian Shield, species of *Notropis* occur nearly everywhere else on the continent, including the endorheic Ríos Nazas-Aguanaval basin, Mexico, and Gulf Coast drainages as far south as the Rio Pánuco drainage, Mexico (Miller et al. 2005). One of the most widely distributed members of the genus and the type species, the Emerald Shiner, *Notropis atherinoides*, is found from the Mackenzie River in northern Canada, which flows into the Arctic Ocean, in the St. Lawrence River, the Hudson River, and the Mississippi River drainage south to the Gulf of Mexico, and in Gulf Slope drainages from Mobile Basin, Alabama, to Galveston Bay, Texas (Page & Burr 2011). The Emerald Shiner is the northernmost occuring species and the Pygmy Shiner, "*Notropis*" *tropicus*, is the southernmost species, occuring in the Rio Pánuco system, Mexico.

Genus *Cyprinella*

The genus *Cyprinella* contains 30 species (Schönhuth & Mayden 2010). These striking and often colorful fishes display fascinating courtship and mating behaviors (see reproduction section). The southeastern United States is the center of diversity for *Cyprinella*. Species diversity is well understood in this genus, although four widespread taxa (Red Shiner, *Cyprinella lutrensis*; Spotfin Shiner, *Cyprinella spiloptera*; Blacktail Shiner, *Cyprinella venusta*; and Steelcolor Shiner, *Cyprinella whipplei*) exhibit morphological or genetic variation that suggests cryptic species may be subsumed in these taxa (Schönhuth & Mayden 2010). Species of *Cyprinella* occur throughout the Mississippi River basin and surrounding rivers ranging from the Red River of the North, a Hudson Bay drainage in southern Manitoba, Canada; in Atlantic Slope drainages from the St. Lawrence River to the Altamaha River, Georgia; and in Gulf Coast drainages from the Suwannee River, Florida, to the Rio Pánuco, Mexico (Miller et al. 2005; Page & Burr 2011; Fig. 12.2). Species of *Cyprinella* occur in the endorheic Ríos Nazas-Aguanaval basin and the Rio Yaqui, which drains into the Pacific Ocean (Miller et al. 2005). The Spotfin Shiner is the northernmost occurring species and one of the most widespread, inhabiting the Red River of the North, the St. Lawrence River, and drainages of the Great Lakes (except Lake Superior) (Page & Burr 2011). It is also widespread in eastern tributaries of the Mississippi River and present to the west in isolated populations in the Ozark and Ouachita Mountains. The southernmost member, the Red Shiner, also a widely distributed species, ranges from Missouri River tributaries, South Dakota, south to eastern Mexico where it occurs in the Ríos Tamesí and Pánuco (Miller et al. 2005; Page & Burr 2011).

Genus *Alburnops*

The genus *Alburnops* contains 20 species that were formerly included in the genus *Notropis* (Mayden et al. 2006). Much of the species diversity of *Alburnops* is located in the southeastern United States, particularly in the Mobile Basin (Fig. 12.4). *Alburnops* contains at least one undescribed species, and there may be additional undescribed species in the genus. Some species, such as the Rainbow Shiner, *Alburnops chrosomus*, are brilliantly colored when spawning. Species of *Alburnops* occur in Atlantic and Gulf Slope drainages from the Hudson River, New York, almost to the southern tip of Florida and west to the Nueces River, Texas; in the Mississippi River north to Minnesota, and in the Hudson Bay drainages, Red River of the North, Minnesota and Manitoba, and Assiniboine River, Alberta, Saskatchewan, and Mantitoba (Page & Burr 2011). Most species in this group have relatively restricted ranges, although three have large ranges. The River Shiner, *Alburnops blennius*, is widespread, occuring in the Hudson Bay drainages, Red River of the North, the Assiniboine River system, and the Mississippi River system south to the Gulf of Mexico. The Ironcolor Shiner, *Alburnops chalybaeus*, occurs in lowlands of the Atlantic Slope and east Gulf Slope from the Hudson River, New York, to southern Florida and west to the Sabine River, Louisiana and Texas, western drainages of the Mississippi embayment, with isolated populations in the San Marcos River, Texas, the Illinois River system, Illinois and Indiana, the Wisconsin River and Lake Winnebago system, Wisconsin, and Lake Michigan drainages, Michigan and Indiana. The Weed Shiner, *Alburnops texanus*, occurs in Gulf Coast drainages from the Suwannee River, Florida and Georgia, to the Nueces River, Texas; in western tributaries of the Mississippi River in the Mississippi Embayment; in the upper Mississippi River system in Minnesota, Iowa, Wisconsin, Illinois, Indiana, and Michigan; and in the Hudson Bay drainage in the Red River of the North, Minnesota (Lee et al. 1980; Page & Burr 2011).

Genus *Gila*

The genus *Gila* contains 18 species and has much of its diversity in Pacific Slope drainages of western North America, although a few taxa inhabit Gulf of Mexico drainages (Fig. 12.3). The Colorado River system contains the highest number of *Gila* species, including the Humpback Chub, *Gila cypha*, and Bonytail Chub, *Gila elegans* (Fig. 12.56e). Colorado River species get quite large (>300 mm SL) (Lee et al. 1980) and can live >40 years (Minckley 1991a; Table 12.5a), clearly an advantage in desert rivers that exhibit unpredictable annual flow patterns. Species of *Gila* occur from the upper Missouri River basin, Montana, where the Utah Chub, *Gila atraria*, has been introduced; the upper Snake River; the Sacramento–San Joaquin River system, California; the Lake Bonneville system, Utah; the Colorado River system, and a number of smaller Pacific Coast drainages of southern California and northern Mexico (Fig. 12.3). Species of *Gila* also occur in the upper Rio Grande, New Mexico, and Rio Conchos, Mexico. The Utah Chub is the northernmost species native to the upper Snake River, Idaho and Wyoming; the Lake Bonneville Basin, Utah; and the Sevier River system, Idaho and Utah; and has been introduced to the upper Missouri system, Montana (Lee et al. 1980; Page & Burr 2011). The southernmost species is the Nazas Chub, *Gila conspersa*, which is restricted to the endorheic Ríos Nazas-Aguanaval basin, Mexico (Miller et al. 2005).

Genus *Lythrurus*

The genus *Lythrurus* contains 11 species, although additional cryptic taxa may be present in this group (Pramuk

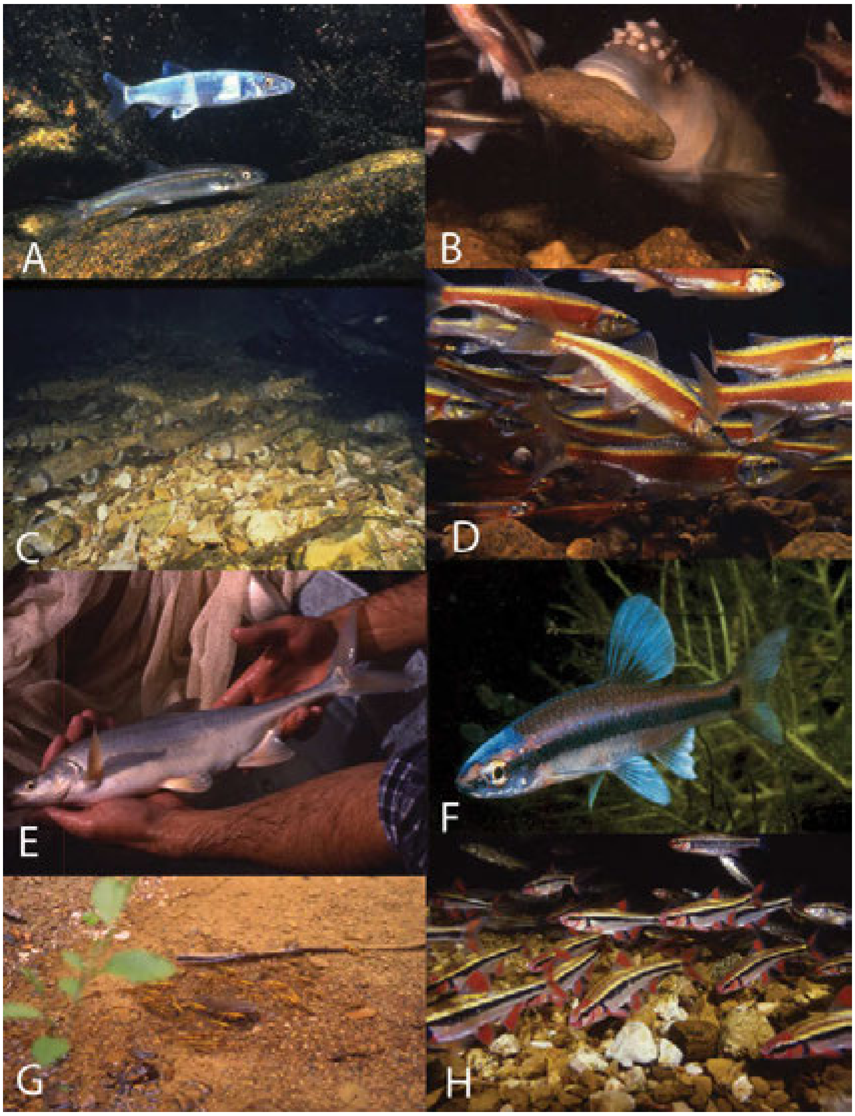


Figure 12.56. (A) Spotfin Chub, *Erimonax monachus*, male (*top*) and female (*bottom*) (photograph by and used with permission of N. M. Burkhead). (B) Bluehead Chub, *Nocomis leptocephalus*, constructing nest (photograph by and used with permission of W. N. Roston). (C) Central Stoneroller, *Campostoma anomalum*, school of tuberculate males (photograph by and used with permission of W. N. Roston). (D) Rosyside Dace, *Clinostomus funduloides*, school of adults in spawning color (photograph by and used with permission of W. N. Roston). (E) Bonytail Chub, *Gila elegans*, Dexter Fish Hatchery, New Mexico (photograph by and used with permission of B. M. Burr). (F) Bluehead Shiner, *Pteronotropis hubbsi*, breeding secondary male (photograph by and used with permission of W. N. Roston). (G) Blackside Dace, *Chrosomus cumberlandensis*, spawning over nest of Creek Chub, *Semotilus atromaculatus* (photograph by and used with permission of R. R. Cicerello). (H) Bleeding Shiner, *Luxilus zonatus*, school of adults in spawning color (photograph by and used with permission of W. N. Roston).

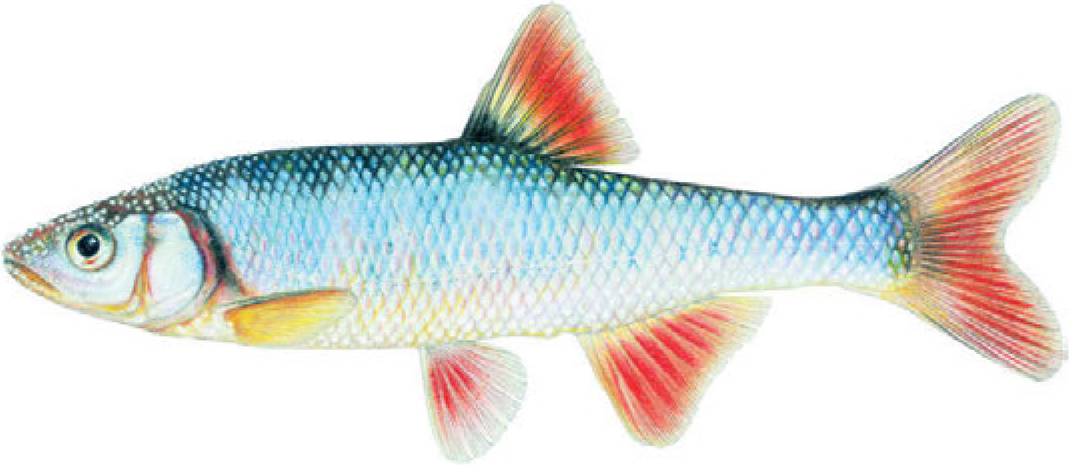


Plate 12.5. Scarlet Shiner, *Lythrurus fasciolaris*

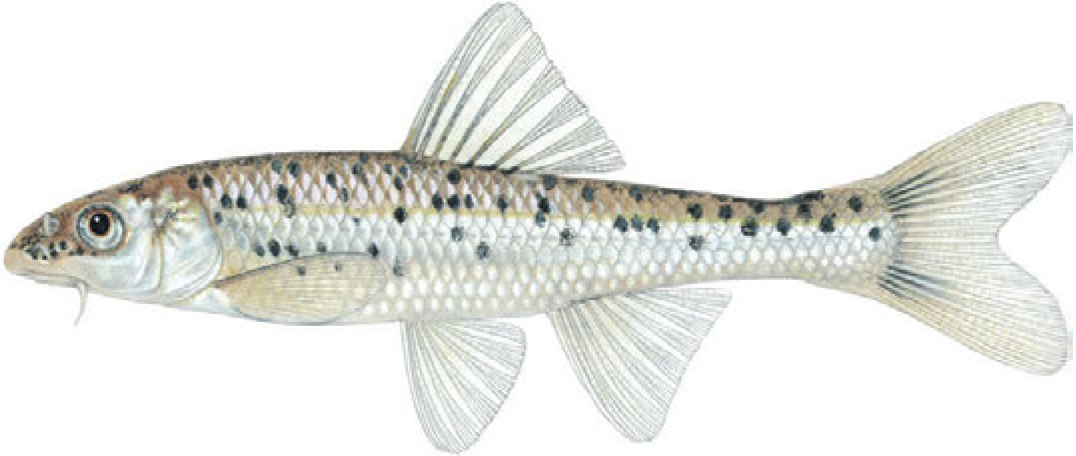


Plate 12.6. Speckled Chub, *Macrhybopsis aestivalis*

et al. 2007). Species of *Lythrurus* are widely distributed throughout much of the Mississippi River basin and in Gulf Coast drainages from the Navidad River, Texas, east to the Chattahoochee River, Alabama and Georgia (Lee et al. 1980; Pramuk et al. 2007; Fig. 12.5). The Redfin Shiner, *Lythrurus umbratilis*, is the most widespread species in the genus, occurring in the Mississippi and Ohio River basins, southern Great Lakes drainages, and Gulf Coast drainages west to the San Jacinto River, Texas (Page & Burr 2011). Other members occupy much smaller ranges, such as the Ouachita Mountain Shiner, *Lythrurus snelsoni*, which is restricted to tributaries of the Little River, Arkansas and Oklahoma, above the Fall Line (Taylor & Lienesch 1996; Page & Burr 2011).

Genus *Macrhybopsis*

The genus *Macrhybopsis* contains eight described and three undescribed species. These fishes inhabit large, often turbid rivers across the eastern United States. Often found over sandy substrates, these fishes have relatively small eyes, elongate maxillary barbels, and many tastebuds across the surface of the body. Species of *Macrhybopsis* occur in Hudson Bay drainages from the Assiniboine and Red Rivers of the North in Manitoba south to Minnesota; in several rivers draining into Lake Erie; in suitable habitat throughout the Mississippi River system from Minnesota south to the Gulf of Mexico, and from the upper Ohio River, New York and Pennsylvania, west to the Republican River of western Nebraska; and in Gulf Coast drainages from the Mobile Basin west to the Rio Grande (Lee et al. 1980; Eisenhour 2004; Fig. 12.6). The Silver Chub, *Macrhybopsis storeriana*, is the most widespread species in the genus, ranging from Hudson Bay drainages in the North to the lower Mississippi River basin and Mobile Basin in the south and from the Kansas River drainage in southern Nebraska to the upper Ohio River drainage, New York. Three species, in the Mobile Basin and other Gulf Coast drainages, Alabama and Florida, are undescribed and additional cryptic species may exist in this genus (Eisenhour 2004).

Genus *Pteronotropis*

The genus *Pteronotropis* contains 10 species (Suttkus & Mettee 2001; Mayden et al. 2006; Page & Burr 2011). With the exception of the Redeye Chub, *Pteronotopis harperi*, male *Pteronotropis* are colorful with enlarged dorsal and anal fins (Fig. 12.56f). Species of *Pteronotropis* occur in swamps and streams of the Atlantic and Gulf Coasts and in the Mississippi Embayment from the Red and Ouachita River drainages of Arkansas and Texas in the west, along the lower reaches of Gulf Coast drainages, much of Florida and north along the Atlantic Slope to the Pee Dee River, South Carolina (Lee et al. 1980; Boschung & Mayden 2004; Page & Burr 2011; Fig 12.7). An isolated population of the Bluehead Shiner, *Pteronotropis hubbsi*, was present in Wolf Lake, southwest Illinois, but is now extirpated (Burr & Warren 1986a).

Genus *Luxilus*

The genus *Luxilus* contains nine species distributed across much of the eastern United States (Fig. 12.8). Two widespread species occupy most of the range of this genus. The Common Shiner, *Luxilus cornutus*, occurs from southern Canada south to central Nebraska in the west and southern Virginia in the east, and the Striped Shiner, *Luxilus chrysocephalus*, occurs in southern Great Lakes drainages, the Mississippi River basin, south to the Gulf Coast and in

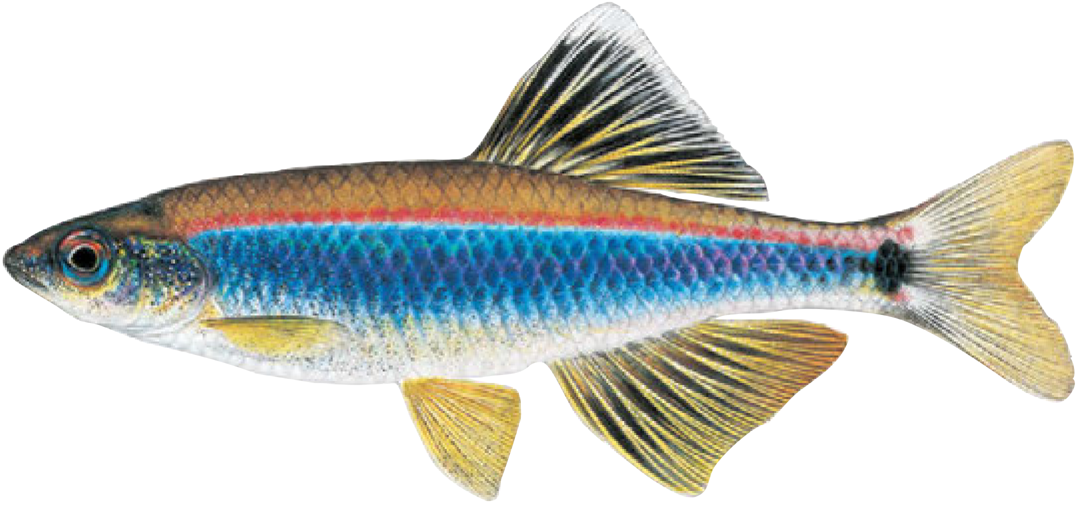


Plate 12.7. Aplachee Shiner, *Pteronotropis grandipinnis*

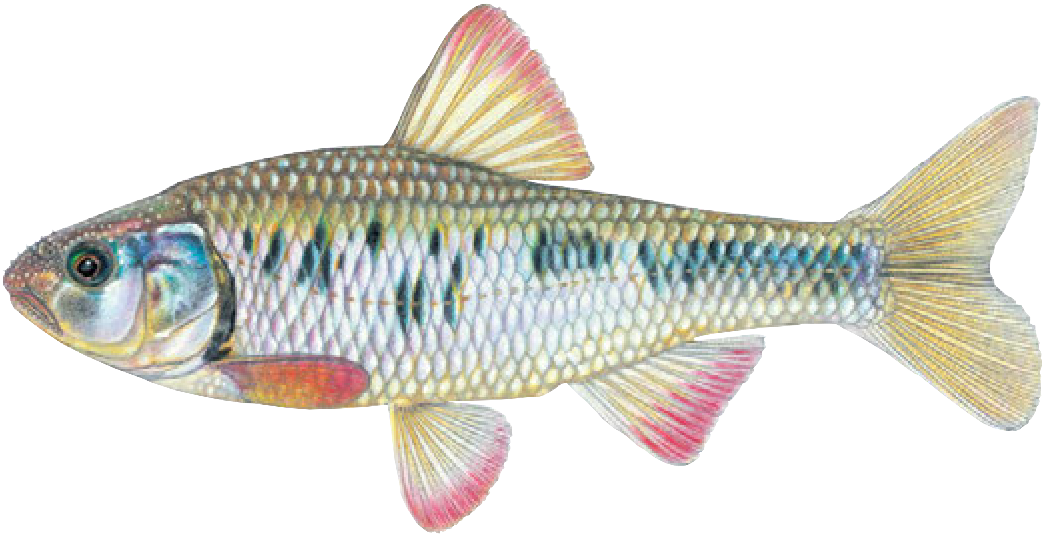


Plate 12.8. Striped Shiner, *Luxilus chrysocephalus*

Gulf Coast drainages from the Mobile Basin west to Lake Ponchartrain (Lee et al. 1980; Page & Burr 2011). The ranges of these two species overlap in some places and hybridization is reported (see genetics section).

Cyprinids as Non-Natives

Cyprinids are popular in the aquarium trade, and a number are important fishes in aquaculture. As a result, a number of non-indigenous species have been released in North America, although few have become established. Unfortunately, the few that are established have either caused or have the potential to cause substantial damage to aquatic ecosystems. In addition to exotic species, a large number of North American species have been introduced (transplanted) outside their native range in North America. At least 104 exotic and native cyprinid species may have been introduced outside their native range, although it often is unclear if the actual introductions occurred and in other cases little or no environmental impact is identified (Fuller et al. 1999). Here, we focus on cyprinid species that are widely established outside their native range or that have the potential to negatively impact native species and the systems they inhabit (see genetics section).

The spread of non-native cyprinids occurs via a number of mechanisms. Several species were stocked intentionally. Stocking may be used to develop a fishery (e.g., Common Carp, *Cyprinus carpio*) or to provide forage for gamefishes (e.g., Red Shiner, *Cyprinella lutrensis*, and Fathead Minnow, *Pimephales promelas*) (Fuller et al. 1999). Other species are stocked in restricted areas such as aquaculture facilities and subsequently escape; examples include the recent escapes of species of three genera of large Asian carps: *Hypopthalmichthys*, *Ctenopharyngodon*, and *Mylopharyngodon* (Schofield et al. 2005). Baitbucket introductions, fishes used as bait and deliberately or accidentally released, account for the spread of many native fishes outside of their native range, particularly the Golden Shiner, *Notemigonus crysoleucas* (Fig. 12.40), and the Fathead Minnow, both favored as baitfishes (Litvak & Mandrak 1993). There is a baseless perception among some anglers that releasing unused baitfish benefits the environment (Litvak & Mandrak 1993). Cyprinids may also be spread as stock contaminants with fish that are stocked intentionally (e.g., Fathead Minnow) (Woodling 1985).

Once released, non-native cyprinids may disperse throughout a river system and in some cases become so common that they are considered native. For example, the Common Carp, a native of Eurasia, is sometimes referred to as the native carp in parts of the Midwest. Competition or predation may restrict the spread of cyprinids. For example, multiple predators (Sculpins, Cottidae; Sacramento Pikeminnow, *Ptychocheilus grandis*, also introduced) restrict the range and distribution of introduced Speckled Dace, *Rhinichthys osculus*, in the Eel River, California (Harvey et al. 2004).

Possibly the first exotic fish species to be released in North America was the ornamental Goldfish, *Carrassius auratus*, originally native to Asia. These apparently were first introduced in the late 1600s (Dekay 1842), and repeated introductions have occurred since then. Although Goldfish are captured widely in North America, locations for established reproducing populations are scattered and localized (Schofield et al. 2005). They appear to establish in highly degraded habitats (Fuller et al. 1999), but continuing introductions complicate the picture.

The Common Carp was introduced into North America in the late 1800s. This species was stocked intentionally and widely and is established throughout much of southern Canada (Scott & Crossman 1973), the United States (Schofield et al. 2005), and Mexico (Miller et al. 2005). Common Carp cause a tremendous amount of damage to the environment, especially when feeding. Their rooting feeding mode disrupts the sediment and uproots aquatic plants, often significantly impacting water quality (Roberts et al. 1995; Titus et al. 2004; Miller & Crowl 2006).

Two species of *Hypopthalmichthys* have been introduced into North America: Silver Carp, *Hypopthalmichthys molitrix*, and Bighead Carp, *Hypopthalmichthys nobilis*. These large Asian carps were introduced by the aquaculture industry to improve water quality in Catfish ponds and to provide an additional aquaculture crop (Fuller et al. 1999; Schofield et al. 2005). Both species feed on plankton and have the potential to compete with large native planktivores (e.g., Paddlefish, *Polyodon spathula*), and they may have the ability to alter plankton communities with negative impacts on invertebrates and other fishes (Sampson et al. 2009). Both are established in the Mississippi River and its larger tributaries such as the Missouri and Ohio Rivers and are steadily increasing their distribution. Significantly, they may invade other river systems, including the St. Lawrence River system and the Mobile Basin via navigation canals, causing substantial ecological disruption in the process. Silver Carp are also well known for their habit of leaping clear of the water when startled and have injured boaters.

Black Carp, *Mylopharnyngodon piceus*, another native of Asia, were introduced by the aquaculture industry to control snails infested with parasites in Catfish ponds. Black Carp feed on invertebrates, particularly mollusks, and thus can reduce the numbers of snails that serve as the intermediate host for a trematode that parasitizes Catfish (Schofield et al. 2005). Black Carp may have established reproductive populations in the lower Mississippi River and are considered a major threat not only to endangered freshwater mussels and snails but to the entire mollusk fauna in the Mississippi River system (Nico et al. 2005).

Grass Carp, *Ctenopharyngodon idella*, yet another Asian native, were introduced to North America by the aquaculture industry to control macrophytes. These large carp can consume up to 45 kg/day of plant material (Fuller et al. 1999) and have been eagerly cultivated and stocked by state agencies as well as aquaculturists because of their ability to control macrophytes (Mitzner 1978). Grass Carp are likely the source of introduction of the Asian tapeworm, *Bothriocephalus opsarichthydis*, to North America (Hoffman & Schubert 1984; Ganzhorn et al. 1992). Grass Carp have been stocked widely within the United States but are established only in the Mississippi River basin and in the Trinity River, Texas (Schofield et al. 2005).

The Tench, *Tinca tinca*, a Eurasian native, was introduced to North America by the U.S. Fisheries Commission in 1877. Several subsequent introductions have occurred, and although Tench were widely stocked, they did not become widely established (Schofield et al. 2005). Reproductive populations occur in the Connecticut River system, Massachusetts and Connecticut; parts of the upper Columbia River system, British Columbia, Idaho, and Washington; the upper Colorado River system, Colorado; the Salinas River system, California; and localities around Puget Sound, Washington.

The Rudd, *Scardinius erythropthalmus*, a Eurasian species, has been widely introduced and transported as a baitfish (Litvak & Mandrak 1993). Numerous baitbucket introductions have occurred, particularly in New England and the south-central United States (Schofield et al. 2005). The Rudd is difficult to distinguish from the Golden Shiner, which is native to North America but also widely introduced outside its native range (Fuller et al. 1999), and thus the overall extent of Rudd introduction and establishment is not clear. Established reproductive populations are present in Arkansas, Maine, Massachussetts, Michigan, Missouri, Nebraska, New York, Ontario, Texas, Virginia, and Washington (Litvak & Mandrak 1993; Schofield et al. 2005).

The Bitterling, *Rhodeus sericeus*, a Eurasian species, was introduced into the Sawmill and Bronx Rivers, New York, sometime before 1923 (Lee et al. 1980). This species, which deposits its eggs in freshwater mussels, persists in the Bronx River. Apparently its numbers are decreasing coincident with decreasing water quality, which is impacting the freshwater mussel population (Schoefield et al. 2005).

The Red Shiner, *Cyprinella lutrensis*, a North American cyprinid native to the central United States and eastern Mexico, has been widely introduced outside its range in the Mobile Basin, Colorado River system, San Joaquin River, California, as well as the Yadkin and Roanoke Rivers (Schoefield et al. 2005). This species preys on larval cyprinids, including the endangered Colorado Pikeminnow, *Ptychocheilus lucius* (Bestgen 1996). Red Shiners are also thought to compete with other endangered native fishes (Rinne 1991) and act as vectors of the Asian tapeworm that is a threat to endangered cyprinids (Brouder 1999; Choudhury et al. 2004; Pullen et al. 2009).

The Fathead Minnow, *Pimephales promelas*, another North American native, is widely produced for use as a baitfish (see commercial importance section) and has also been stocked outside its native range as a forage fish. The native range is difficult to determine but likely included much of North America east of the Rocky Mountains (Fuller et al. 1999). It has been introduced and is now widespread in drainages along the Pacific Coast from southern British Columbia to California (Lee et al. 1980; Fuller et al. 1999).

The Golden Shiner, another North American native, is also widely used as a baitfish (see commercial importance section) and is widely distributed in southeastern Canada and the eastern United States (Lee et al. 1980; Fig. 12.40). This may be its native range, although this is unclear. The Golden Shiner was introduced intentionally into the Colorado and Sacramento River systems as a forage fish for introduced gamefishes (Lee et al. 1980; Sigler & Sigler 1987).

PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships of North American cyprinids have been and continue to be confused. The confusion is a function of the large number of species and their apparent morphological conservatism. An historical proliferation of generic and specific names has resulted in complex synonymies. Lack of a coherent philosophy governing the field of systematics and the inability of investigators to deal with large numbers of characters, particularly in such a species-rich group, contributed further to

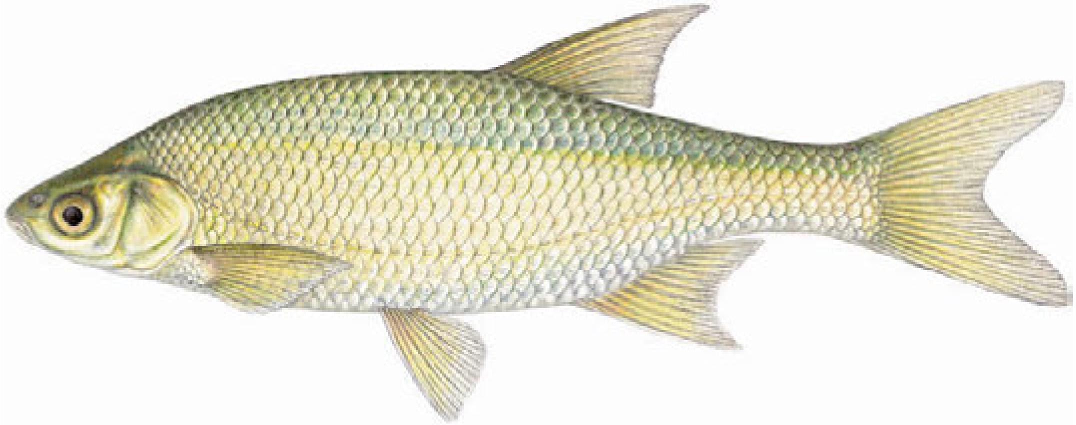


Plate 12.9. Golden Shiner, *Notemigonus crysoleucas*

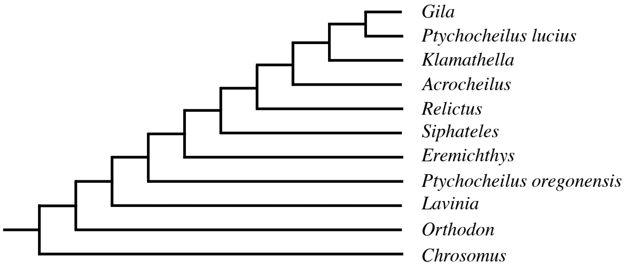
the confusion for much of the 20th century. Phylogenetic systematics (Hennig 1966) dealt with the first problem; the development of computer algorithms and rapid increases in computing power have helped with the second. These changes, coupled with the recent ability to access large numbers of molecular characters, have dramatically clarified cyprinid relationships. We anticipate that future work, particularly multi-locus, species-tree analyses (see Hollingsworth & Hulsey 2011), will dramatically transform our understanding of North American cyprinid relationships.

Two major clades of cyprinids represented in the North American fauna are generally recognized by cyprinid systematists: the leucisins, containing the single species Golden Shiner, *Notemigonus crysoleucas*, and the phoxinins, containing all remaining species (Cavender & Coburn 1992; Coburn & Cavender 1992). Relationships among phoxinins are being resolved gradually, but several major questions still remain unanswered regarding phylogenetic relationships of North American cyprinids. Notably, what are the relationships among species, and are the currently recognized genera monophyletic? What are the relationships among major clades of North American cyprinids? Are the North American phoxinins a monophyletic group?

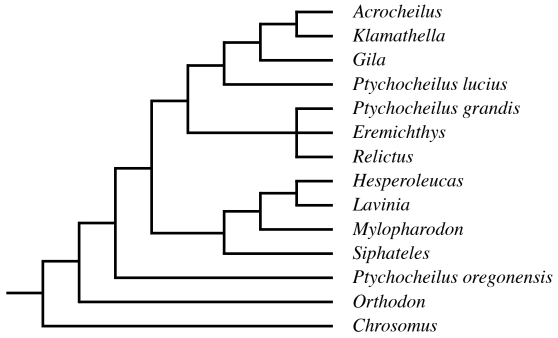
In the mid-1900s, the North American cyprinid fauna was considered to contain two distinct groups, a western fauna and an eastern fauna. The western fauna contained taxa native to the Pacific Slope, and the eastern fauna contained taxa native to the Mississippi River basin, other Gulf of Mexico drainages, and Atlantic Slope drainages. This view persisted even though several taxa did not conform to this pattern. The genera *Rhinichthys* and *Clinostomus* (Fig. 12.56d) were both considered members of the western fauna even though they are distributed widely east of the Pacific Divide (Figs. 12.51 and 12.15, respectively), and the genus *Oregonichthys* was considered part of the eastern fauna even though it is native to Pacific Slope drainages (Fig. 12.42). The classification of North American cyprinids reflected the tensions in systematic biology. Classifications represented a compromise between evolutionary history and convenience (Mayr 1953), and unsurprisingly, this led to nomenclatural instability and confusion. The tensions in systematic biology were reflected in the different approaches taken by Carl Hubbs and Reeve Bailey, both major figures in North American cyprinid systematics. Hubbs's work focused on morphological differences between taxa, but Bailey concentrated on similarities. In the 1950s, Bailey dramatically revised the classification of several groups of North American cyprinids (Bailey 1951, 1956). He synonymized several genera based on a few morphological characters that included the presence and position of a maxillary barbel, scalation, and gut morphology. Several workers responded negatively to these taxonomic changes (Lachner & Jenkins 1967; McPhail & Lindsey 1970; Jenkins & Lachner 1971). Hubbs & Miller (1977:275) stated: “It is abundantly obvious that much of the generic placement in American cyprinids is in a chaotic state, and that the prime significance attributed to intestinal coiling vs. the single compressed-S configuration, and to the presence vs. absence of a maxillary barbel, in the taxonomy of the group has been very considerably discredited.” Nevertheless, Bailey's changes had a profound impact on classification. Taxonomic changes that he made in two footnotes in identification keys (Bailey 1951, 1956) now require large amounts of data to overturn.

The first explicitly phylogenetic analysis of relationships among North American cyprinids was Mayden's

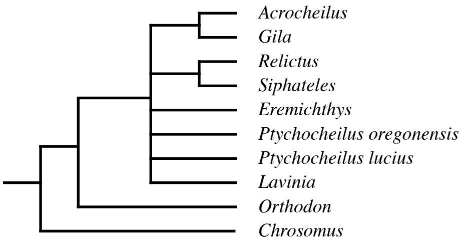
(1989) examination of relationships in *Cyprinella* based largely on morphological characters. In order to clarify the appropriate outgroups to polarize characters within *Cyprinella*, he examined a large number of cyprinid taxa. Ironically, the phylogeny produced by his search for outgroup taxa has had a greater impact on cyprinid systematics than his phylogeny of *Cyprinella*. Mayden recognized a large monophyletic group of primarily eastern cyprinids (but also including the genera *Oregonichthys* and *Richardsonius*, both found in Pacific Slope drainages) (Figs. 12.42 and 12.50) that he referred to as the open posterior myodome (OPM) clade. This clade was supported by a single synapomorphy (shared, derived character), an opening in the floor of the posterior myodome bounded by the parasphenoid and the basioccipital (Coburn 1982). Further, he made several taxonomic recommendations to maintain consistency with his hypothesized phylogenetic relationships. He removed the genera *Cyprinella*, *Luxilus*, *Lythrurus*, and *Pteronotropis* from synonymy with *Notropis* and dismembered the genus *Hybopsis*, recognizing the genera *Erimystax*, *Extrarius*, *Macrhybopsis*, and *Platygobio*.


Gila
Ptychocheilus lucius
Klamathella
Acrocheilus
Relictus
Siphateles
Eremichthys
Ptychocheilus oregonensis
Lavinia
Orthodon
Chrosomus

A) Simons et al. 2003


Acrocheilus
Klamathella
Gila
Ptychocheilus lucius
Ptychocheilus grandis
Eremichthys
Relictus
Hesperoleucas
Lavinia
Mylopharodon
Siphateles
Ptychocheilus oregonensis
Orthodon
Chrosomus

B) Smith et al. 2002


Acrocheilus
Gila
Relictus
Siphateles
Eremichthys
Ptychocheilus oregonensis
Ptychocheilus lucius
Lavinia
Orthodon
Chrosomus

C) Bufalino & Mayden 2010b

Figure 12.57. Hypotheses of relationships in the western clade. (A) Bayesian analysis of mitochondrial 12S and 16S rRNA sequences (redrawn from Simons et al. 2003). (B) Parsimony analysis of mitochondrial cytochrome *b* sequences (redrawn from Smith et al. 2002). (C) Bayesian analysis of nuclear Rag1 and S7 sequences (redrawn from Bufalino & Mayden 2010b).

Coburn & Cavender (1992) produced the most comprehensive phylogenetic hypothesis based on morphology to date. They included representatives of nearly all North American cyprinids and recognized three major clades: the western clade, the chub clade, and the shiner clade. Members of Mayden's OPM clade were distributed among these clades. This was due to the use of different character systems and also disagreement between Coburn & Cavender (1992) and Mayden (1989) over interpretation of some characters, including the OPM (Simons & Mayden 1999). Their analysis also included a number of Asian phoxinins, including the genera *Tribolodon* and *Rhynchocypris*; these were part of their chub clade (Coburn & Cavender 1992).

The relationships of North American phoxinins have been investigated using DNA sequences of the mitochondrial 12S and 16S ribosomal RNA genes (Simons & Mayden 1997, 1998, 1999; Simons et al. 2003) and the nuclear Rag1 and S7 genes (Schönhuth et al. 2008; Bufalino & Mayden 2010ab; Schönhuth & Mayden 2010). These analyses consistently identified three major clades: western clade, Creek Chub + plagopterin clade, and OPM clade. Simons et al. (2003) considered the OPM clade sister to the Creek Chub + plagopterin clade with these sister to the western clade; however, Bufalino & Mayden (2010) could not resolve sister-group relationships among these three groups. These clades differed in various ways from the clades identified by Coburn & Cavender (1992) and Mayden (1989). A phylogeny of western cyprinids based on mitochondrial cytochrome *b* sequences (Smith et al. 2002) was largely consistent with Simons et al. (2003) and Bufalino & Mayden (2010ab).

The western clade contains the genera *Acrocheilus*, *Chrosomus*, *Eremichthys*, *Gila*, *Hesperoleucas*, *Klamathella*, *Lavinia*, *Mylopharodon*, *Orthodon*, *Ptychocheilus*, *Relictus*, and *Siphateles* (Fig. 12.57). The genus *Chrosomus* is the sister to all other taxa in the western clade (Bufalino & Mayden 2010b; Simons & Mayden 1998; Smith et al. 2002) and is the only member of this group present in eastern North America (Fig. 12.14). The genus *Orthodon* is the sister to all other members of the western clade, but little consensus of relationships of the remaining genera is present among the various analyses (Fig. 12.57). The Moapa Dace, *Gila coriacea*, was classified formerly in the monotypic genus *Moapa* because of its distinctive appearance (Hubbs & Miller 1948), but Smith et al. (2002) considered it a member of *Gila* based on their analysis (Fig. 12.57b). Smith et al. (2002) resurrected the genus *Klamathella* from synonymy with *Gila* (Fig. 12.57b), and Simons & Mayden (1999) and Simons et al. (2003) considered the genus *Klamathella* to be sister to the rest of *Gila* (Fig. 12.57a); Smith et al. (2002) considered *Klamathella* sister to *Acrocheilus* (Fig. 12.57b). We concur with the resurrection of *Klamathella*. The pikeminnows, genus *Ptychocheilus*, may not be a monophyletic group. Mitochondrial data place the Colorado Pikeminnow, *P. lucius*, as either closely related to *Gila* (Fig. 12.57a) (Simons & Mayden 1998; Simons et al. 2003) or sister to the *Klamathella* + *Acrocheilus* + *Gila* clade (Fig. 12.57ab) (Smith et al. 2002). Nuclear gene data provide little resolution to this issue (Fig. 12.57c) (Bufalino & Mayden 2010b).

The Creek Chub + plagopterin clade contains the genera *Couesius*, *Lepidomeda*, *Meda*, *Plagopterus*, *Margariscus*, *Hemitremia*, and *Semotilus* (Dowling et al. 2002; Simons et al. 2003: Fig 12.58). This is a small clade that presents a complex problem. The genera *Couesius*, *Margariscus*, *Hemitremia*, and *Semotilus* are similar morphologically; however, no unequivocal morphological features unite this group. *Couesius*, *Margarsiscus*, and *Semotilus* have a short, triangular, preterminal maxillary barbel, although the barbel is missing in some individuals and populations (McPhail & Lindsey 1970; Scott & Crossman 1973; Jenkins & Burkhead 1994). *Semotilus* and *Hemitremia* are recovered consistently as sister-taxa in analyses of morphological (Coburn & Cavender 1992) and molecular (Simons & Mayden 1997; Simons et al. 2003; Bufalino & Mayden 2010ab) data (Fig. 12.58bc). These four genera form a monophyletic group in maximum likelihood and Bayesian analyses of mitochondrial 12S and 16S ribosomal RNA genes (Simons et al. 2003) and nuclear Rag1 and S7 genes (Bufalino & Mayden 2010b) (Fig. 12.58bc). Parsimony analysis of the same data set revealed they were paraphyletic with respect to the plagopterins. Resolution of relationship of *Semotilus* + *Hemitremia*, *Couesius*, and *Margariscus* varied depending on weights applied to various character transformations (Simons & Mayden 1997). Unweighted morphological (Coburn & Cavender 1992) and molecular analyses of the mitochondrial cytochrome *b* gene and the Rag1 and S7 nuclear genes (Dowling et al. 2002; Bufalino & Mayden 2010ab) also resulted in paraphyly of these taxa (Fig. 12.58a).

The plagopterins, or spine-fins, contain the genera *Plagopterus*, *Lepidomeda*, and *Meda* (Miller & Hubbs 1960). They are characterized by spine-like rays in the dorsal and pelvic fins; tiny scales; and bright, silvery body coloration. Molecular evidence supported inclusion of the Leatherside Chub, *Lepidomeda copei*, formerly placed in *Gila* and *Snyderichthys*, in the plagopterin group (Simons & Mayden 1997), a relationship alluded to by Miller & Hubbs (1960:6): "Resemblance is particularly close between *Lepidomeda* and several species referred to the genus *Gila*, and even more strikingly with a species of the Bonneville system, *copei* that has been referred to a monotypic genus (Miller 1945). It is not now apparent whether such relationship extending even to details of coloration is indicative of intimate relationship." A study of cytochrome *b* variation across the range of *L. copei* revealed evidence for two clades, a northern clade in the Snake and Bear Rivers of Idaho and Wyoming, respectively, and

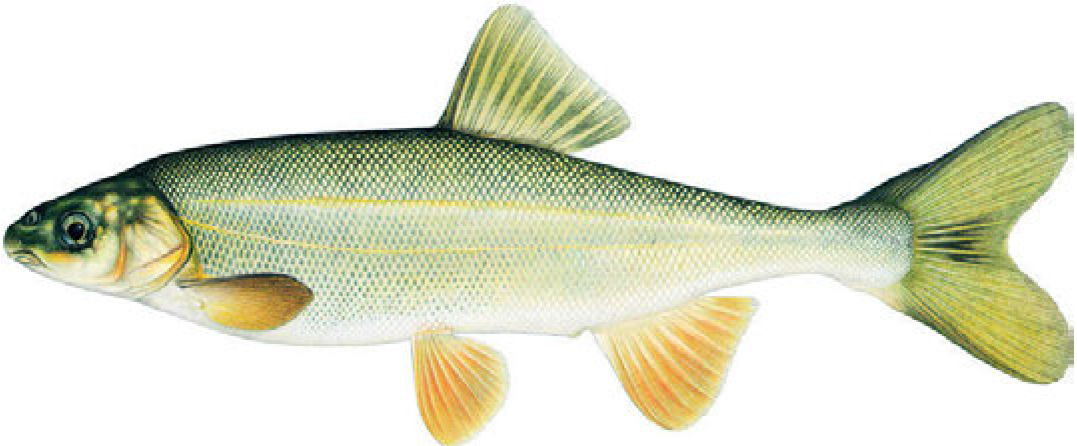


Plate 12.10. Chiselmouth, *Acrocheilus alutaceus*

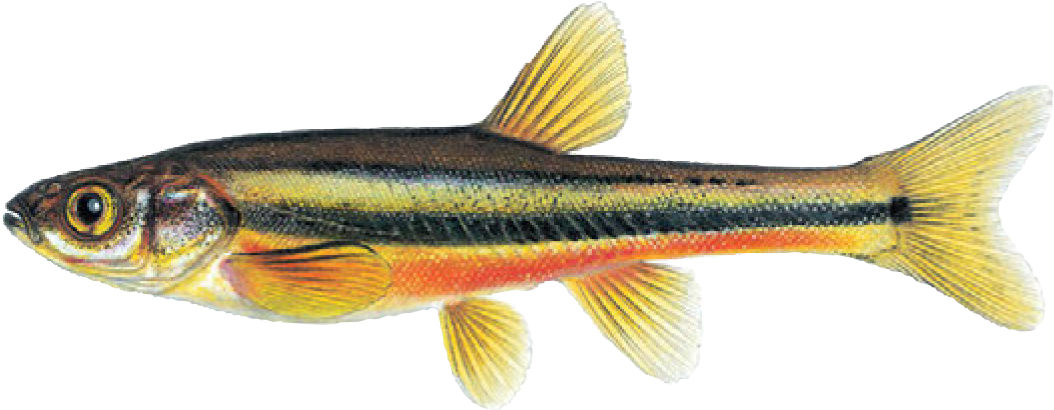


Plate 12.11. Northern Redbelly Dace, *Chrosomus eos*

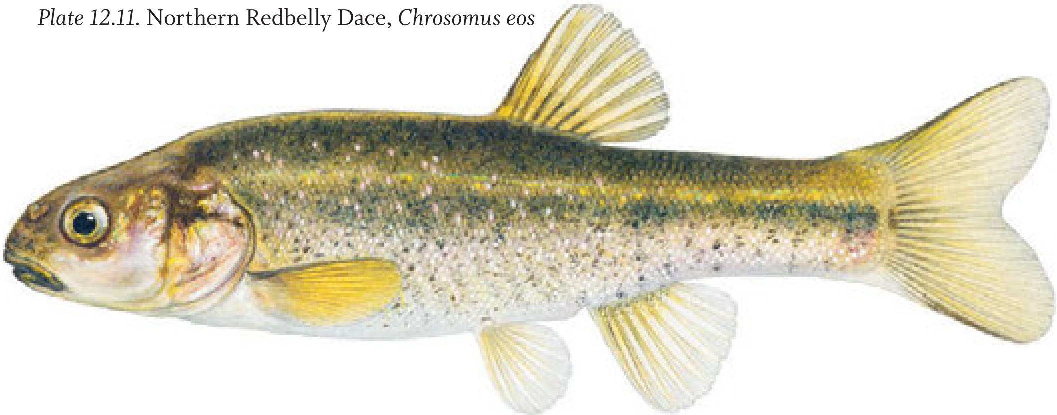


Plate 12.12. Desert Dace, *Eremichthys acros*

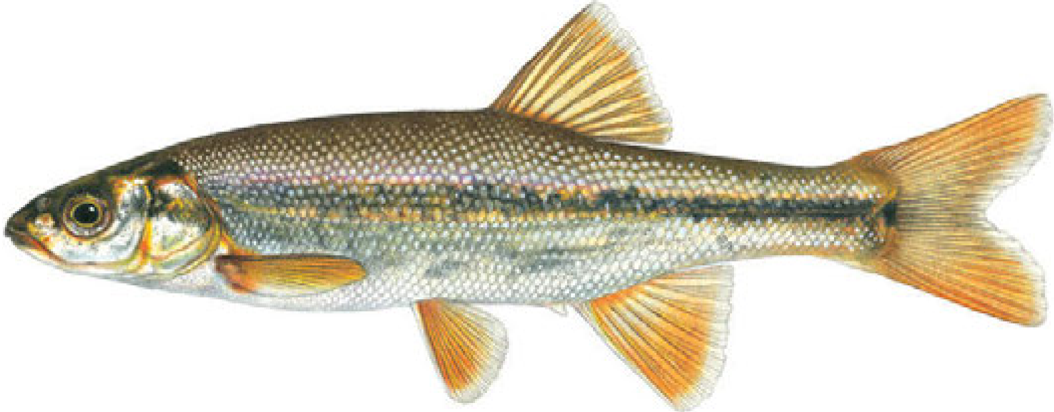


Plate 12.13. California Roach, *Hersperoleucas symmetricus*

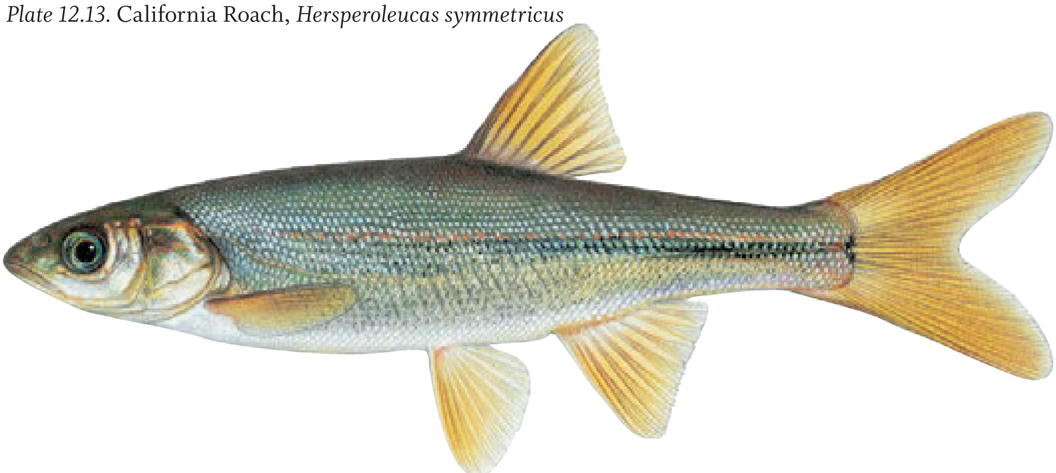


Plate 12.14. Hardhead, *Mylopharodon conocephalus*

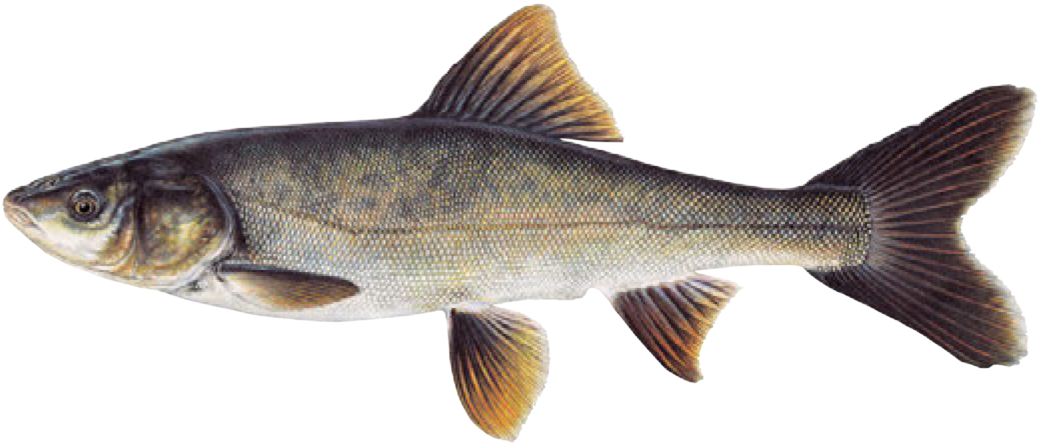


Plate 12.15. Sacramento Blackfish, *Orthodon microlepidotus*

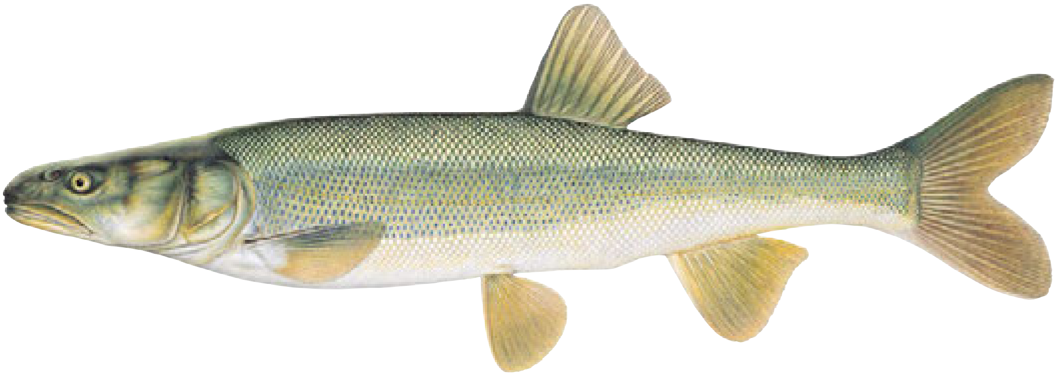


Plate 12.16. Colorado Pikeminnow, *Ptychocheilus lucius*

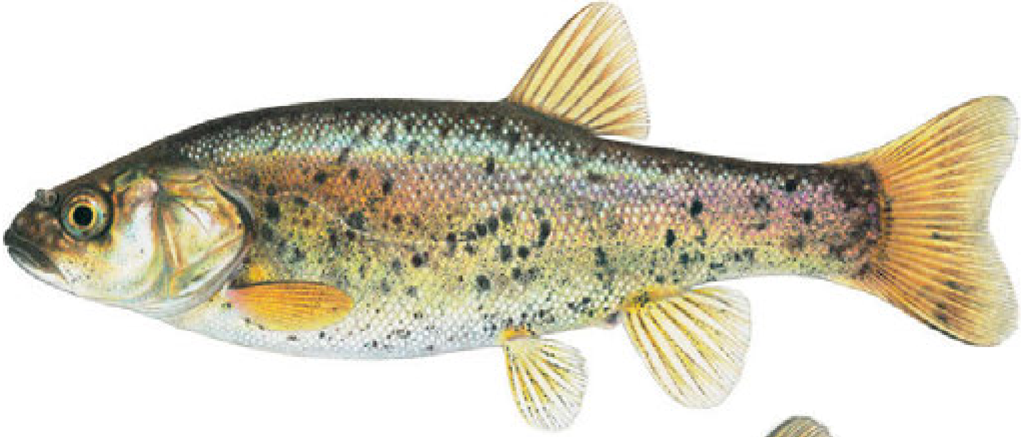


Plate 12.17. Relict Dace, *Relictus solitarius*

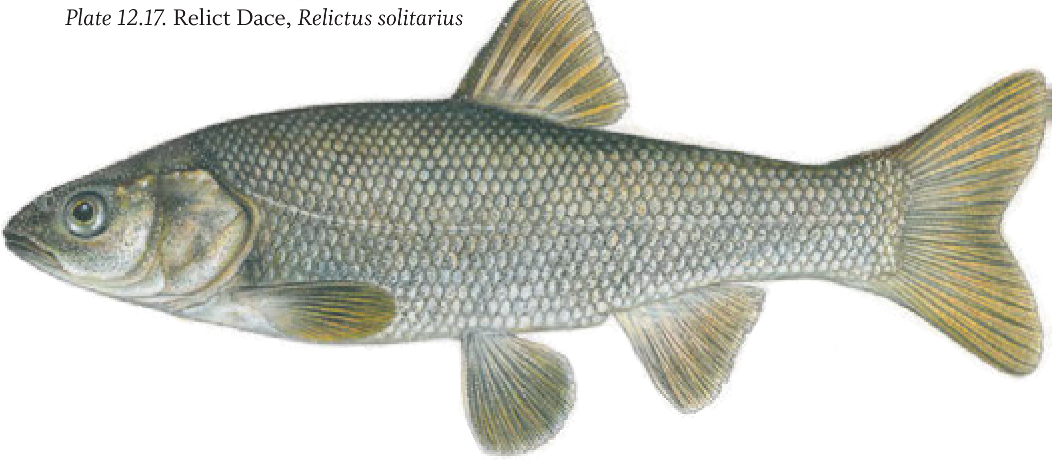
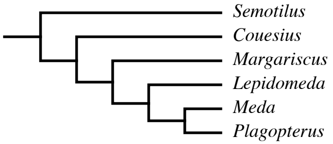
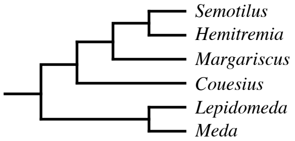


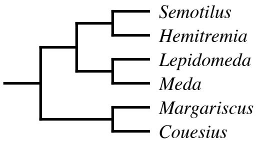
Plate 12.18. Mohave Tui Chub, *Siphateles bicolor mojavensis*


Semotilus
Couesius
Margariscus
Lepidomeda
Meda
Plagopterus

A) Dowling et al. 2002


Semotilus
Hemitremia
Margariscus
Couesius
Lepidomeda
Meda

B) Simons et al. 2003


Semotilus
Hemitremia
Lepidomeda
Meda
Margariscus
Couesius

C) Bufalino & Mayden 2010b

Figure 12.58. Hypotheses of relationships in the creek chub + plagopterin clade. (A) Parsimony analysis of mitochondrial cytochrome *b* sequences (redrawn from Dowling et al. 2002). (B) Bayesian analysis of mitochondrial 12S and 16S rRNA sequences (redrawn from Simons et al. 2003). (C) Bayesian analysis of nuclear Rag1 and S7 sequences (redrawn from Bufalino & Mayden 2010b).

a southern clade in the Utah Lake drainage and Sevier River of Utah (Johnson & Jordan 2000; Dowling et al. 2002). In an analysis of plagopterin relationships including representatives from both clades, *L. copei* was polyphyletic; *Lepidomeda mollispinis* (Virgin Spinedace), *Lepidomeda albivallis* (White River Spinedace), and *L. copei* from the Snake and Bear River drainages formed an unresolved trichotomy sister to *Lepidomeda vittata* (Little Colorado Spinedace). This group was sister to *L. copei* from the Sevier River and Utah Lake drainages (Dowling et al. 2002). Mitochondrial and nuclear DNA sequences, morphology, and ecology present compelling evidence that there are two species of the Leatherside Chub, the Southern Leatherside Chub, *Lepidomeda aliciae*, and the Northern Leatherside Chub, *Lepidomeda copei* (Johnson et al. 2004). The genus *Lepidomeda* is the sister-taxon to *Meda* plus *Plagopterus* (Fig. 12.58a) (Dowling et al. 2002).

For ease of discussion, the OPM clade is divided into four groups, including a paraphyletic basal grade of taxa and three monophyletic clades: *Platygobio* clade, *Phenacobius* clade, and shiner clade. Simons & Mayden (1999) discussed

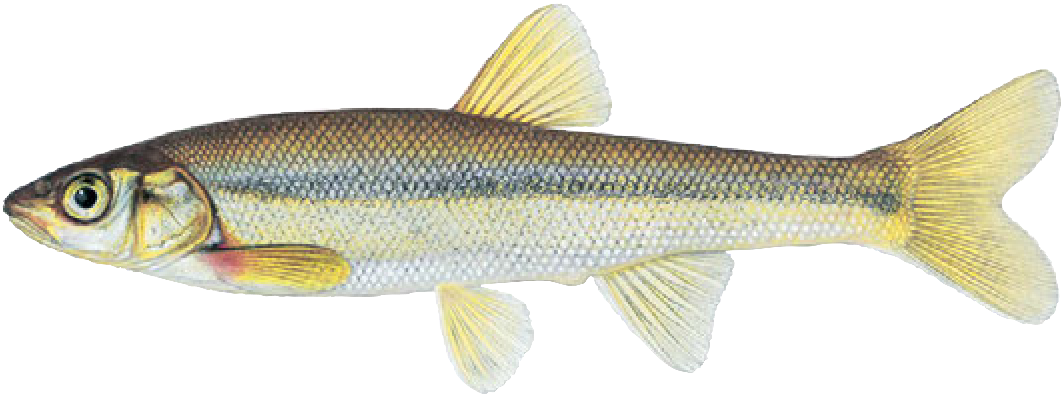


Plate 12.19. Lake Chub, *Couesius plumbeus*

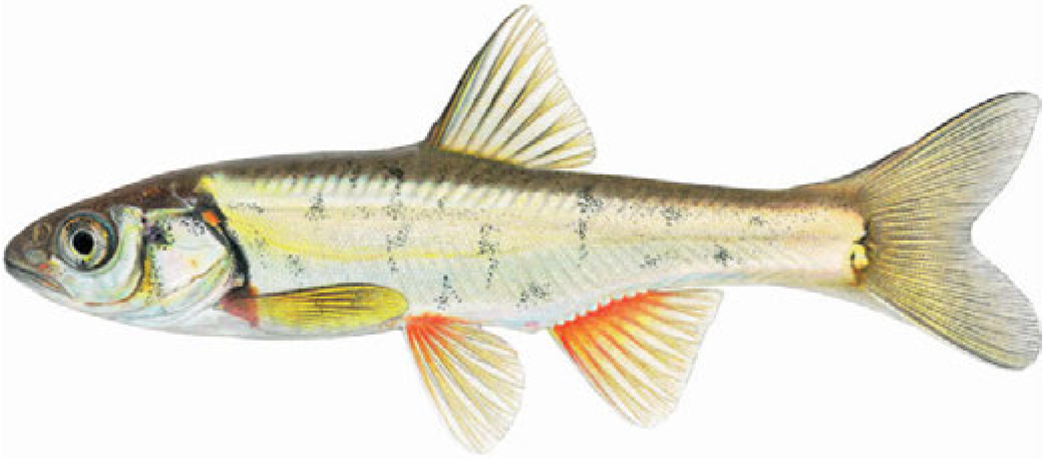


Plate 12.20. White River Spinedace, *Lepidomeda albivallis*

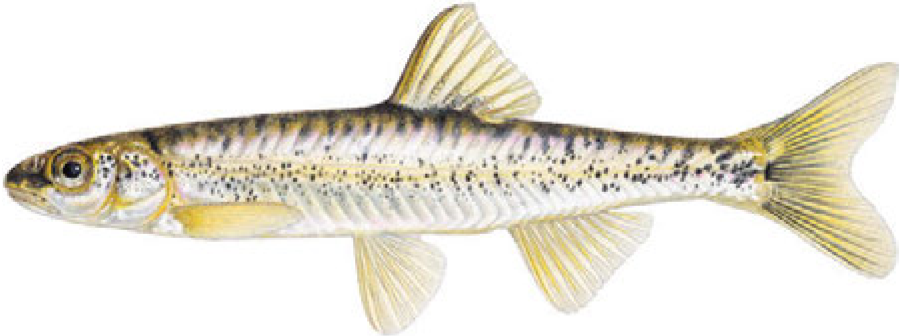


Plate 12.21. Spikedace, *Meda fulgida*

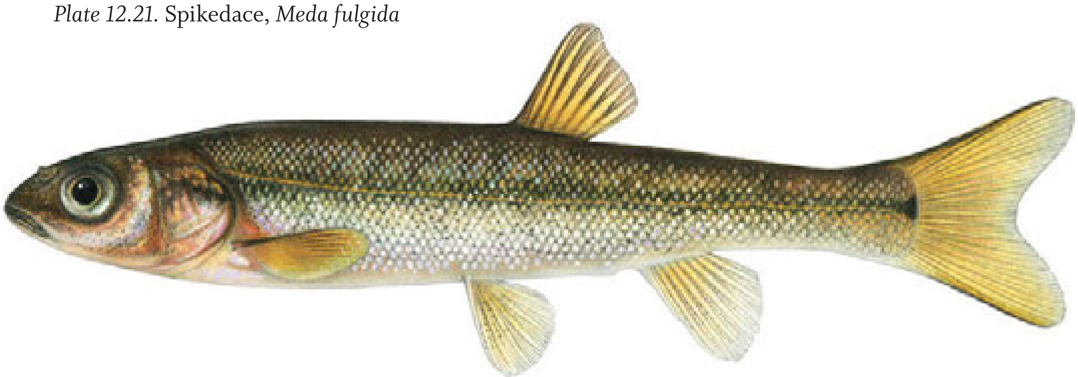


Plate 12.22. Pearl Dace, *Margariscus margarita*

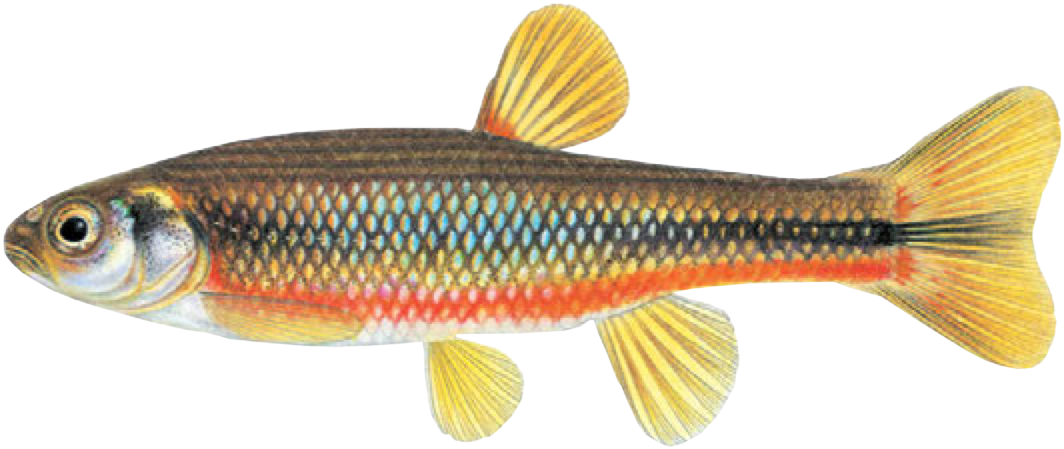


Plate 12.23. Flame Chub, *Hemitremia flammea*

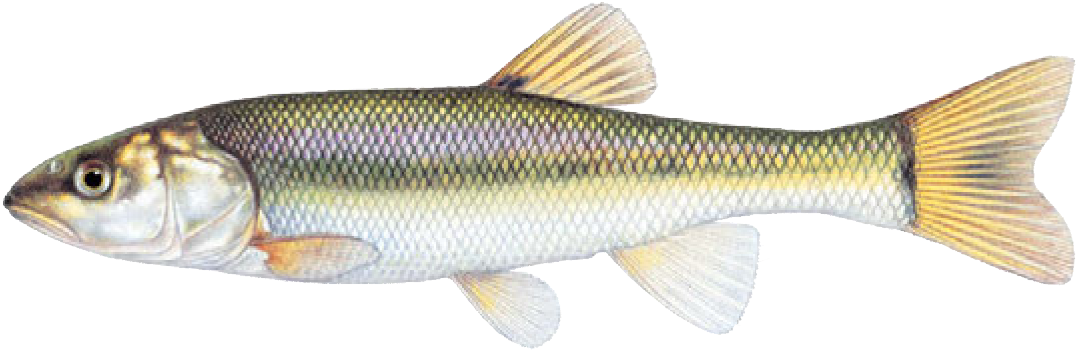
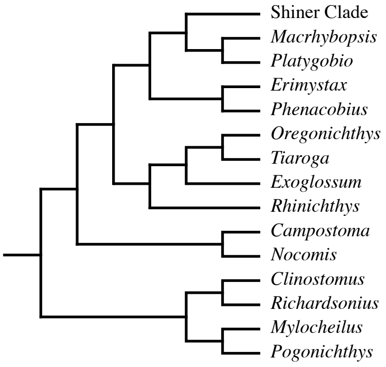


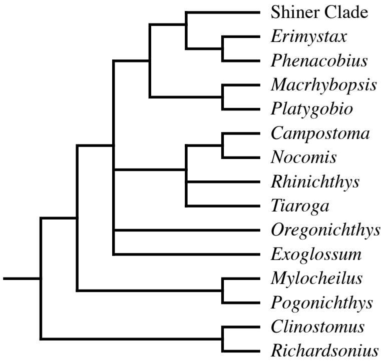
Plate 12.24. Creek Chub, *Semotilus atromaculatus*

the homology of the OPM and the inclusion of taxa not identified by Mayden (1989) as members of this group. The OPM clade is the largest group of North American cyprinids, and much work remains to adequately resolve the relationships among the included taxa, thus the classification and relationships described here are necessarily preliminary. The basal grade contains the genera *Campostoma*, *Clinostomus*, *Exoglossum*, *Iotichthys*, *Mylocheilus*, *Nocomis*, *Oregonichthys*, *Pogonichthys*, *Rhinichthys*, *Richardsonius*, and *Tiaroga* (Smith et al. 2002; Simons et al. 2003; Bufalino & Mayden 2010ab). Simons et al. (2003) divided these taxa into a series of clades, but not all these are supported by nuclear data (Bufalino & Mayden 2010ab); however, some groups are always recovered (Fig. 12.59).

The *Phenacobius* clade contains the genera *Erimystax* and *Phenacobius* (Dimmick 1993; Simons et al. 2003; Hollingsworth & Hulsey 2011). Mayden (1989) described a hypothesis of relationship among included species based on morphological data. Dimmick & Burr (1999) examined species relationships in *Phenacobius* using data from morphology, allozymes, and DNA sequences. Simons (2004) described relationships among species in *Erimystax* based on analysis of mitochondrial cytochrome *b* sequences. Hollingsworth & Hulsey (2011) used a multi-locus, coalescent-based approach, corroborating a sister-group relationship between *Phenacobius* and *Erimystax* but recovered a different species-level phylogeny in *Phenacobius* than that of Mayden (1989) and Dimmick & Burr (1999). The *Phenacobius* clade is either sister to the *Platygobio* clade plus the shiner clade (Fig. 12.59a) (Simons et al. 2003) or to the shiner clade (Fig. 12.59b) (Bufalino & Mayden 2010b). Schönhuth & Mayden (2010) placed *Erimystax* in the shiner clade (see shiner clade below).



A) Simons et al. 2003



B) Bufalino & Mayden 2010

Figure 12.59. Hypotheses of relationships in the open posterior myodome clade. (A) Bayesian analysis of mitochondrial 12S and 16S rRNA sequences (redrawn from Simons et al. 2003). (B) Bayesian analysis of nuclear Rag1 and S7 sequences (redrawn from Bufalino & Mayden 2010b).

The *Platygobio* clade contains two genera, *Macrhybopsis* and *Platygobio*. Placed in *Hybopsis* by Bailey (1951), these taxa were classified subsequently in three genera: *Extrarius*, *Macrhybopsis*, and *Platygobio* (Mayden 1989). Subsequent authors placed the genus *Extrarius* in *Macrhybopsis* (Coburn & Cavender 1992; Dimmick 1993; Simons & Mayden 1999). Relationships within *Macrhybopsis* are not well resolved. Dimmick (1993) placed the Sturgeon Chub, *Macrhybopsis gelida*, plus the Sicklefin Chub, *Macrhybopsis meeki*, as sister to the *M. aestivalis* complex. Eisenhour (1999) reviewed the systematics of the Peppered Chub, *Macrhybopsis tetranema*, and Eisenhour (2004) described variation in the *M. aestivalis* complex, elevating several species from synonymy with the Speckled Chub, *Macrhybopsis aestivalis*. He also presented a hypothesis of relationships based on 17 morphological characters for these species. No comprehensive phylogenetic hypothesis is available for all species in this clade, and several species await description. Substantial support exists for a sister-group between *Platygobio* and *Macrhybopsis* (Fig. 12.59ab) (Simons et al. 2003; Bufalino & Mayden 2010b).

The *Campostoma* clade contains the genera *Campostoma* and *Nocomis*; the phylogenetic position of this group depends on the data and analysis. Bayesian analysis of mitochondrial 12S and 16S sequences places the *Campostoma* clade as sister to a group containing the shiner clade and the genera *Platygobio*, *Macrhybopsis*, *Erimystax*, *Phenacobius*, *Oregonichthys*, *Tiaroga*, *Exoglossum*, and *Rhinichthys* (Fig. 12.59a) (Simons et al. 2003). Bayesian analysis of combined nuclear Rag1 and S7, however, places this clade in a monophyletic group with *Rhinichthys* and *Tiaroga* (Fig. 12.59b) (Bufalino & Mayden 2010b). Similarly, the relationships of *Exoglossum* and *Oregonichthys* vary depending on the data and analysis (Fig. 12.59ab). Resolution of these relationships will require more intensive taxon sampling and additional data.

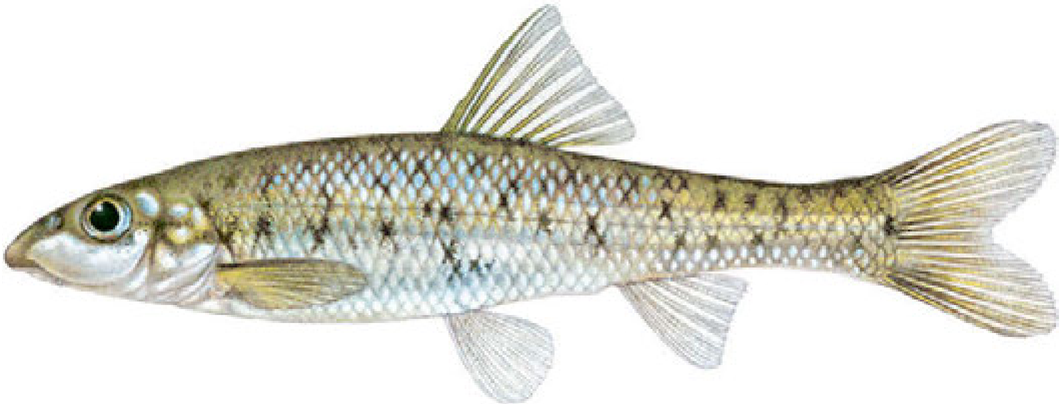


Plate 12.25. Gravel Chub, *Erimystax x-punctatus*

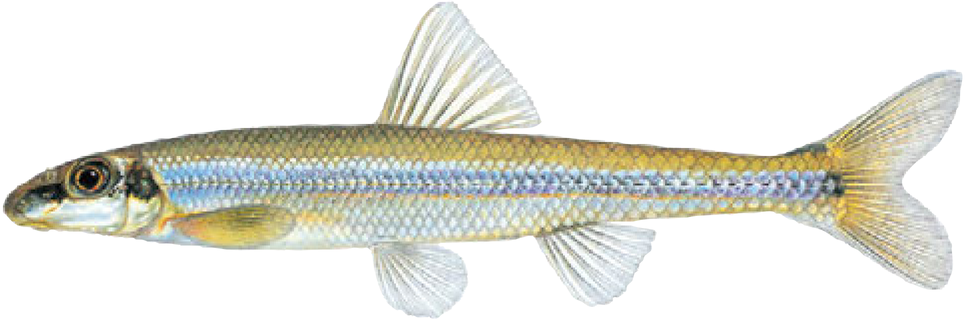


Plate 12.26. Stargazing Minnow, *Phenacobius uranops*

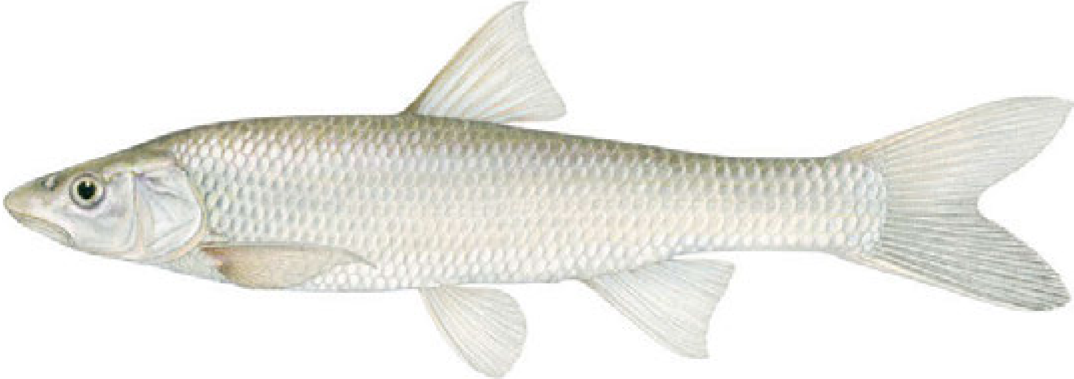


Plate 12.27. Flathead Chub, *Platygobio gracilis*

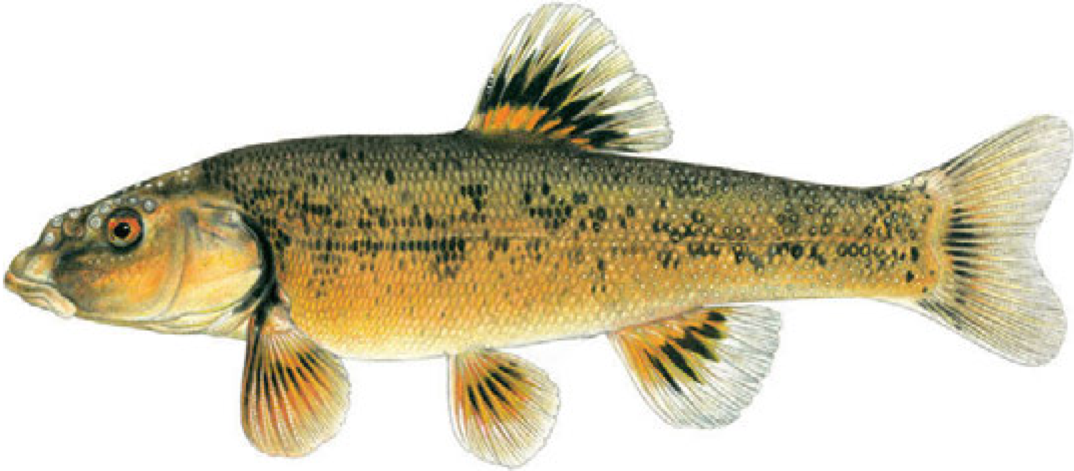


Plate 12.28. Mexican Stoneroller, *Campostoma ornatum*

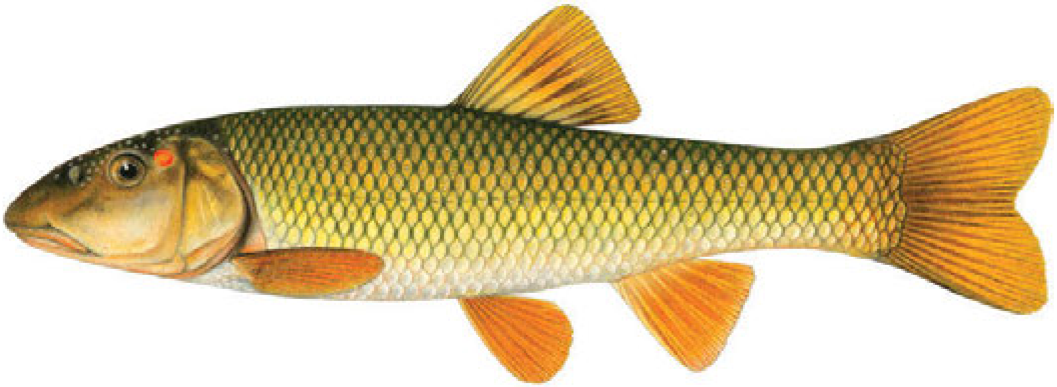


Plate 12.29. Redspot Chub, *Nocomis asper*

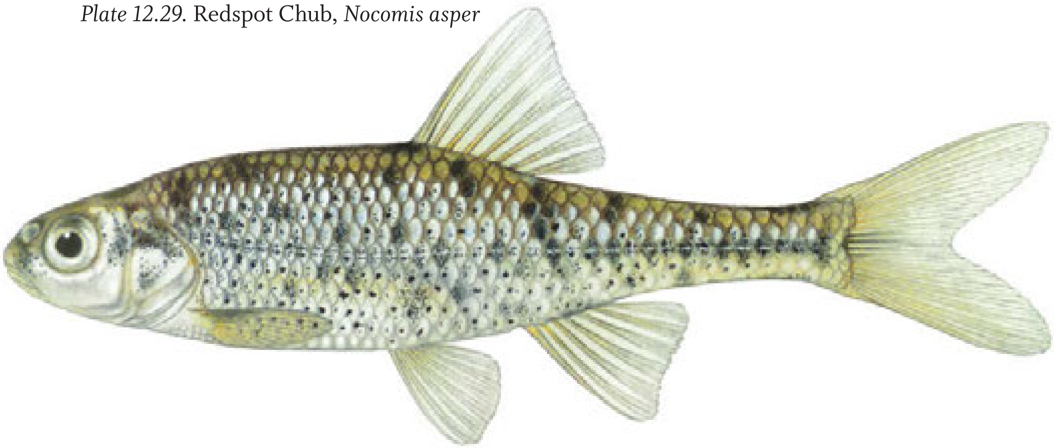


Plate 12.30. Oregon Chub, *Oregonichthys crameri*

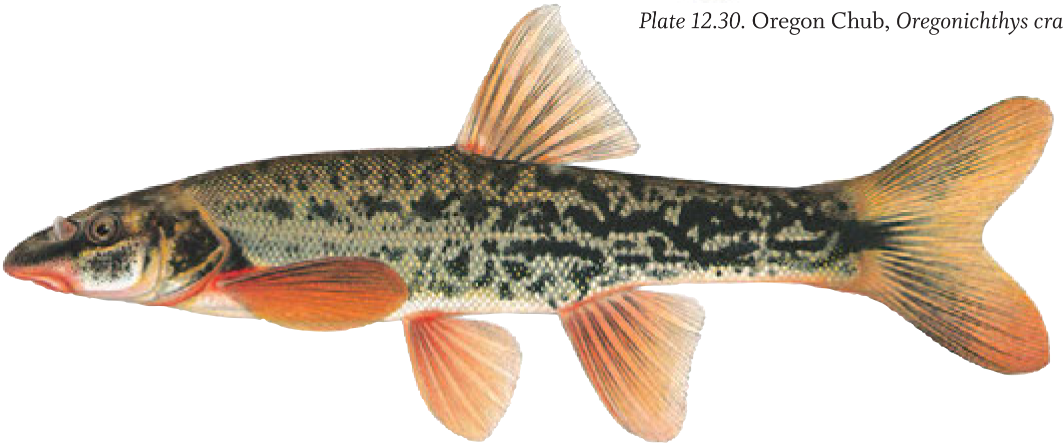


Plate 12.31. Longnose Dace, *Rhinichthys cataractae*

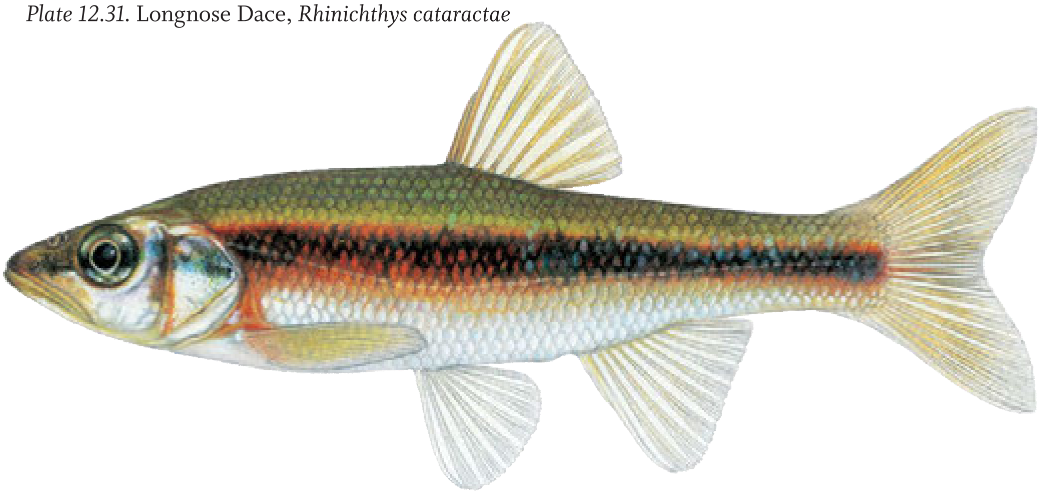


Plate 12.32. Redside Dace, *Clinostomus funduloides*

The genera *Clinostomus* (Fig. 12.56d), *Richardsonius*, *Mylocheilus*, and *Pogonichthys* are in a basal position with respect to the rest of the OPM clade. *Clinostomus* and *Richardsonius* are sister-taxa (Simons & Mayden 1999; Simons et al. 2003; Bufalino & Mayden 2010b), have long been recognized as close relatives (Uyeno 1961b), and have an interesting biogeographical distribution with *Clinostomus* found in eastern North America (Fig. 12.15) and *Richardsonius* found west of the western Continental Divide (Fig. 12.50). *Mylocheilus* and *Pogonichthys* were only recently recognized as close relatives (Simons & Mayden 1999) and occur in western North America where the genus *Mylocheilus* is native to the Columbia River, Oregon, north to the Nass River, British Columbia (Fig. 12.37), and the genus *Pogonichthys* is native to the Sacramento River system, California (Fig. 12.48). *Clinostomus* plus *Richardsonius* are either the sister to all other members of the OPM clade (Fig. 12.59b) (Bufalino & Mayden 2010b) or sister to *Mylocheilus* plus *Pogonichthys* (Fig. 12.59a) (Simons & Mayden 1999; Simons et al. 2003).

The shiner clade contains ≥170 species. This clade, as currently defined, includes the genera *Agosia*, *Alburnops*, *Algansea*, *Aztecula*, *Codoma*, *Cyprinella*, *Dionda*, *Ericymba*, *Erimonax*, *Graodus*, *Hudsonius*, *Hybognathus*, *Hybopsis*, *Luxilus*, *Lythrurus*, *Miniellus*, *Notropis*, *Pimephales*, *Pteronotropis*, *Tampichthys*, and *Yuriria* (Simons et al. 2003; Mayden et al. 2006; Schönhuth et al. 2008). In addition, the genus *Erimystax* (and presumably *Phenacobius*) may also be part of this group (Schönhuth & Mayden 2010). Relationships among these genera are largely unresolved because no single study exists with sufficient taxon and character sampling to produce a well-supported, comprehensive hypothesis of relationships. Several genera were recently elevated from synonymy with *Notropis* and a number of species, although clearly not members of *Notropis*, cannot be assigned to a particular genus; herein these are referred to as "*Notropis*" (following Mayden et al. 2006). Thus, our discussion of relationships must be viewed as provisional, illustrating areas for future research. The shiner clade is well supported based on analysis of mitochondrial 12S and

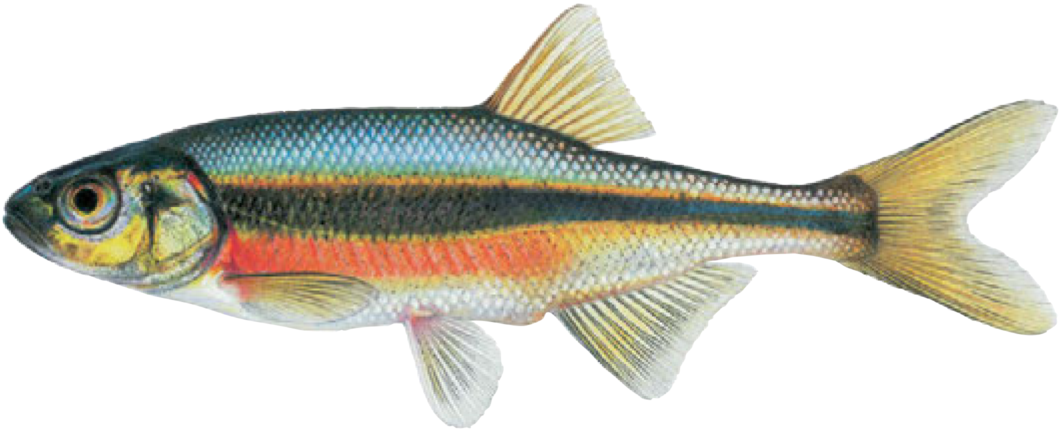


Plate 12.33. Redside Shiner, *Richardsonius balteatus*

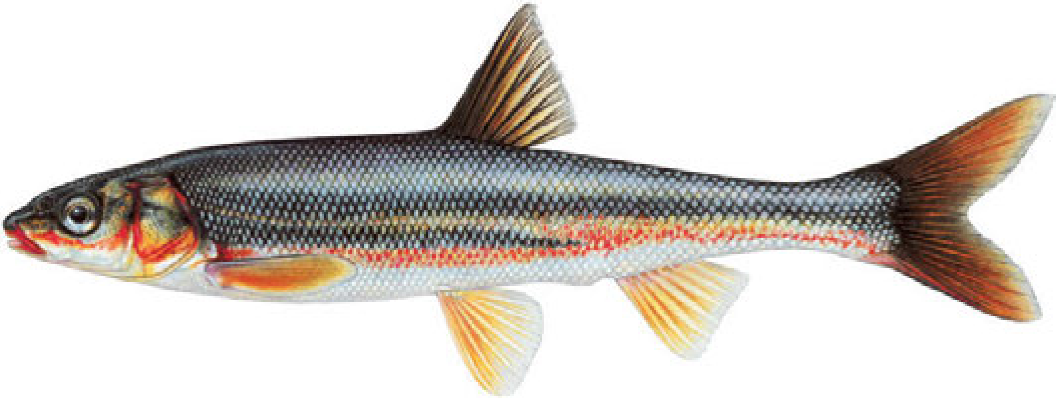


Plate 12.34. Peamouth, *Mylocheilus caurinus*

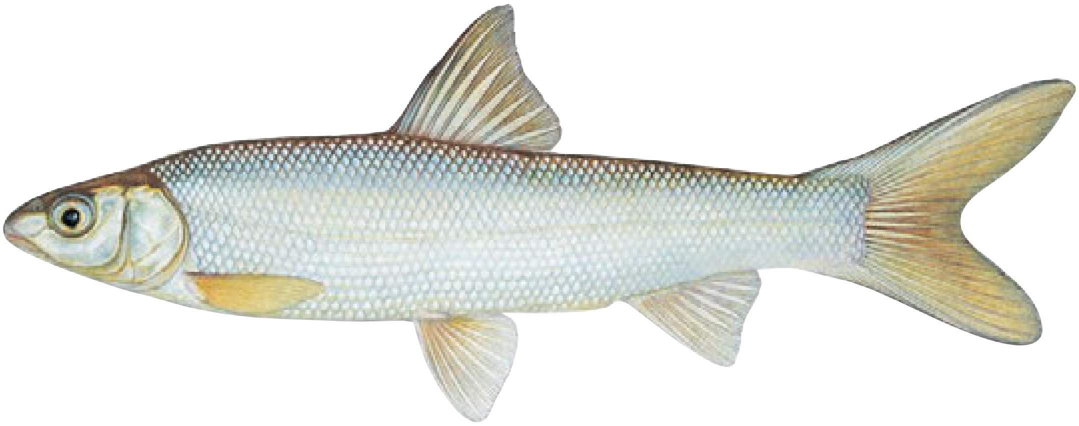


Plate 12.35. Splittail, *Pogonichthys macrolepidotus*

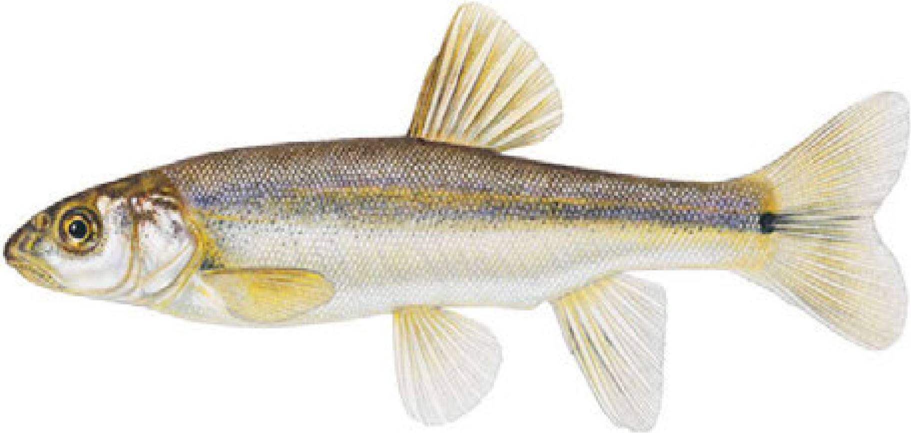


Plate 12.36. Longfin Dace, *Agosia chrysogaster*

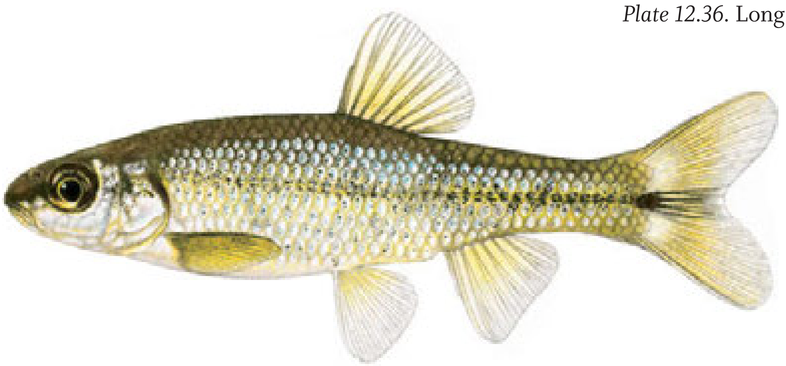
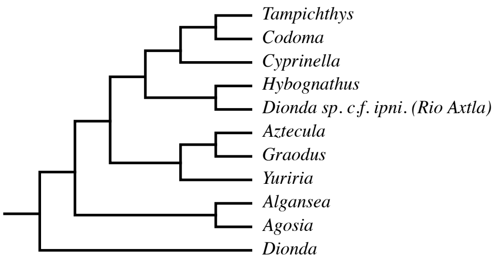


Plate 12.37. Roundnose Minnow, *Dionda episcopa*

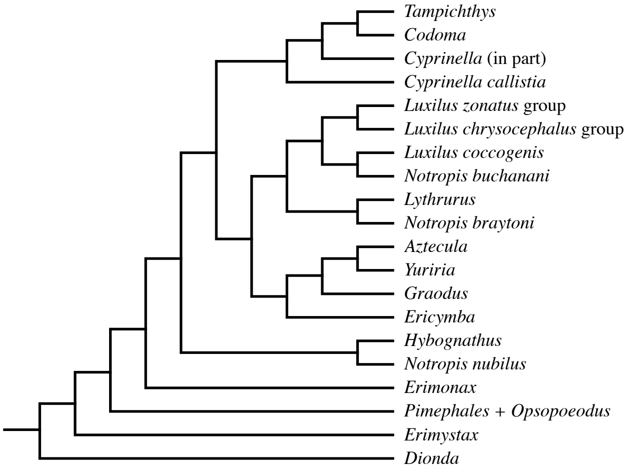
16S ribosomal RNA (Simons et al. 2003); Mayden et al. (2006) included many more taxa in an analysis of mitochondrial cytochrome *b* sequences. This analysis resolved relationships within species groups and illustrated that the genera *Notropis*, *Luxilus*, and *Pteronotropis* are not monophyletic as currently defined. Mayden et al. (2006) resurrected several genera to partially resolve these taxonomic problems. Schönhuth et al. (2008) examined relationships of Mexican shiners in an analysis of one mitochondrial (cytochrome *b*) and three nuclear genes (S7, Rhodopsin, and Rag1) and illustrated that the genus *Dionda* was not monophyletic as currently defined. A new genus, *Tampichthys*, was described to contain species formerly included in *Dionda*, and genera were resurrected to contain taxa formerly classified in *Notropis*. Schönhuth & Mayden (2010) examined the relationships of *Cyprinella* based on separate analyses of mitochondrial cytochrome *b* and nuclear Rag1 genes and included several outgroup taxa that also shed light on relationships in the shiner clade. Papers by Mayden et al. (2006), Schönhuth et al. (2008), and Schönhuth & Mayden (2010) form the basis of the discussion of phylogenetic relationships in the shiner clade (Figs. 12.60–12.62).

The genus *Dionda* is the sister-group to all other shiner taxa included in the Schönhuth et al. (2008) and Schönhuth & Mayden (2010) analyses (Figs. 12.60–12.62). The genus *Dionda* was not included in Mayden et al. (2006), but a sister-group relationship of *Dionda* to all other shiners is not inconsistent with their results. The genus *Agosia* is sister to *Algansea* (Schönhuth et al. 2008). These comprise the sister-group to all other shiners exclusive of *Dionda*; Mayden et al. (2006) did not include *Algansea* but did include *Agosia*. Schönhuth et al. (2008) described interspecific relationships within *Dionda* and *Algansea*. The genera *Aztecula*, *Graodus*, and *Yuriria* form a monophyletic group (Mayden et al. 2006; Schönhuth et al. 2008; Schönhuth & Mayden 2010), but their relationship to the rest of the shiners is unclear (Figs. 12.60–12.62). Schönhuth et al. (2008) and Mayden et al. (2006) described interspecific relationships within these genera. The genus *Codoma* is sister to *Tampichthys* (Schönhuth et al. 2008; Schönhuth & Mayden 2010), and these are closely related to *Cyprinella*, *Miniellus*, and four species: Nazas Shiner, *"Notropis" nazas*; Bigmouth Shiner, *"Notropis" dorsalis*; and Sandbar Shiner, *"Notropis" scepticus*

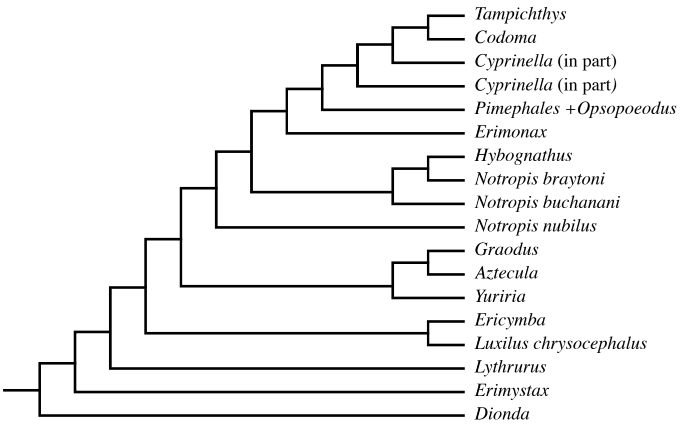

Tampichthys
Codoma
Cyprinella
Hybognathus
Dionda sp. c.f. ipni. (Rio Axtla)
Aztecula
Graodus
Yuriria
Algansea
Agosia
Dionda

Schönhuth et al. 2008

Figure 12.60. Hypothesis of relationships among Mexican cyprinids in the shiner clade. Bayesian analysis of mitochondrial (cytochrome *b*) and nuclear (Rag1, Rhodopsin, Rag1) sequences (redrawn from Schönhuth et al. 2008).

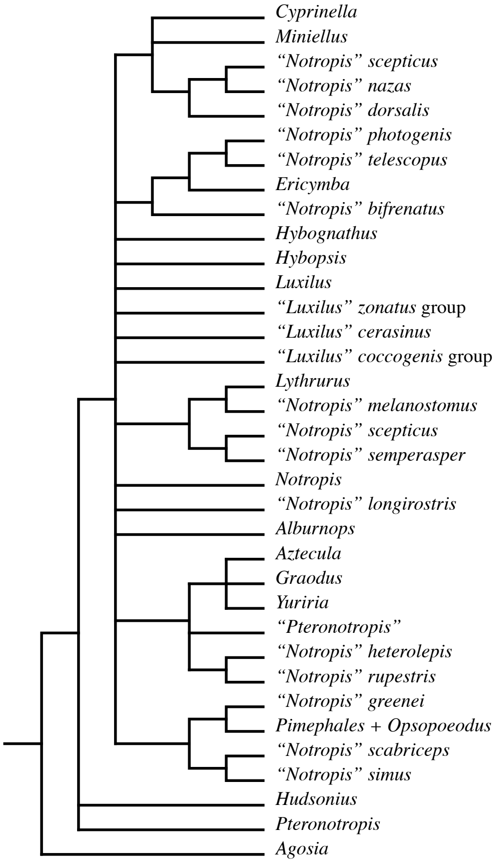

Tampichthys
Codoma
Cyprinella (in part)
Cyprinella callistia
Luxilus zonatus group
Luxilus chrysocephalus group
Luxilus coccogenis
Notropis buchanani
Lythrurus
Notropis braytoni
Aztecula
Yuriria
Graodus
Ericymba
Hybognathus
Notropis nubilus
Erimonax
Pimephales + Opsopoeodus
Erimystax
Dionda

A) Schönhuth & Mayden 2010, Cytochrome *b*


Tampichthys
Codoma
Cyprinella (in part)
Cyprinella (in part)
Pimephales +Opsopoeodus
Erimonax
Hybognathus
Notropis braytoni
Notropis buchanani
Notropis nubilus
Graodus
Aztecula
Yuriria
Ericymba
Luxilus chrysocephalus
Lythrurus
Erimystax
Dionda

B) Schönhuth & Mayden 2010, Rag1

Figure 12.61. Hypotheses of relationships of members of the shiner clade. (A) Maximum likelihood and Bayesian analyses of mitochondrial cytochrome *b* sequences. (B) Maximum likelihood and Bayesian analyses of nuclear Rag1 sequences (redrawn from Schönhuth & Mayden 2010).


Cyprinella
Miniellus
"Notropis" scepticus
"Notropis" nazas
"Notropis" dorsalis
"Notropis" photogenis
"Notropis" telescopus
Ericymba
"Notropis" bifrenatus
Hybognathus
Hybopsis
Luxilus
"Luxilus" zonatus group
"Luxilus" cerasinus
"Luxilus" coccogenis group
Lythrurus
"Notropis" melanostomus
"Notropis" scepticus
"Notropis" semperasper
Notropis
"Notropis" longirostris
Alburnops
Aztecula
Graodus
Yuriria
"Pteronotropis"
"Notropis" heterolepis
"Notropis" rupestris
"Notropis" greenei
Pimephales + Opsopoeodus
"Notropis" scabriceps
"Notropis" simus
Hudsonius
Pteronotropis
Agosia

Mayden et al. 2006

Figure 12.62. Hypotheses of relationships of members of the shiner clade. Bayesian analysis of mitochondrial cytochrome *b* sequences (redrawn from Mayden et al. 2006).

(Mayden et al. 2006). *Codoma* has been considered a close relative of *Pimephales* (Page & Johnston 1990a), *Cyprinella* (Mayden 1989, 2002), and *Tampichthys* (formerly *Dionda*) (Simons et al. 2003). Apparent egg-clustering behavior in *Codoma* (Minckley & Vives 1990) was used as evidence for relationship with *Pimephales*, also an egg clusterer (Page & Johnston 1990; Table 12.4C). Subsequently, S. J. Vives indicated *Codoma* is actually a crevice spawner (pers. comm. cited by Mayden & Simons 2002; Table 12.4A). Mayden (2002) considered *Codoma* a close relative of *Cyprinella* based on morphology (see Mayden 1989), spawning behavior, and molecular data, but Simons et al. (2003) considered *Codoma* a close relative of *Tampichthys* (formerly *Dionda*) based on molecular data. Reproductive behavior also supports this hypothesis as some members of *Tampichthys* are also crevice spawners (Mayden & Simons 2002; Table 12.4C).

Phylogenetic issues associated with *Cyprinella* relationships include relationships among species, membership of the genus, and relationship of *Cyprinella* to other North American cyprinid genera. Most species included in *Cyprinella* are unequivocally members of this group (but see Schönhuth & Mayden 2010; Fig. 12.61) given their distinctive physiognomy and spawning behavior. Other species that have been referred to *Cyprinella* include the Ornate Shiner, *Codoma ornata*; Spotfin Chub, *Erimonax monachu*; Thicklip Chub, *Cyprinella labrosa*; and Santee Chub, *Cyprinella zanema*. Mayden (1989) published a phylogenetic hypothesis of species-level relationships based on morphology and also detailed morphological variation within the clade. He placed *Cyprinella* in a monophyletic group with *Luxilus* and *Lythrurus*. He included the genus *Codoma* within *Cyprinella*, sister to the *C. lutrensis* clade. He referred the Spotfin Chub to *Erimystax* based on barbel morphology and included the Thicklip Chub and Santee Chub in *Hybopsis* based on nine morphological characters. In contrast, Coburn & Cavender (1992) included the Spotfin Chub, Thicklip Chub, and Santee Chub in *Cyprinella*. They placed the genus *Cyprinella* in a monophyletic group with *Opsopoeodus* plus *Pimephales* based on three morphological characters. Their work was focused on generic relationships and thus did not address relationships within *Cyprinella*. Dimmick (1993) used variation in allozymes to examine relationships of barbelled cyprinids, formerly classified in *Hybopsis*. Dimmick identified a sister-group relationship between the Thicklip Chub and Whitetail Shiner, *Cyprinella galactura*. In addition, the Thicklip Chub plus the Santee Chub formed the sister-group to the Bigeye Chub, *Hybopsis amblops*, and the Rosyface Chub, *Hybopsis rubrifrons*. Dimmick's (1993) analysis may suffer from low taxon sampling and choice of outgroup (genus *Campostoma*). Broughton & Gold (2000) examined relationships of species of *Cyprinella* based on mitochondrial ND2 and ND4L genes and found significantly different relationships than did Mayden (1989). No evidence supported inclusion of the Spotfin Chub in *Cyprinella*; however, inclusion of the Thicklip Chub and Santee Chub in *Cyprinella* was supported as in Schönhuth & Mayden (2010). In Simons et al. (2003), no evidence supported a relationship of *Cyprinella* with *Pimephales*, *Opsopoeodus*, or the Spotfin Chub. Parsimony analyses placed *Cyprinella* sister to some species of *Notropis*, but likelihood analyses placed *Cyprinella* as the sister to the rest of the shiner clade. Schönhuth et al. (2008) identified *Cyprinella* as sister to *Codoma* and *Tampichthys* based on their analyses of one mitochondrial and three nuclear genes and this relationship is supported by similarity in spawning behavior

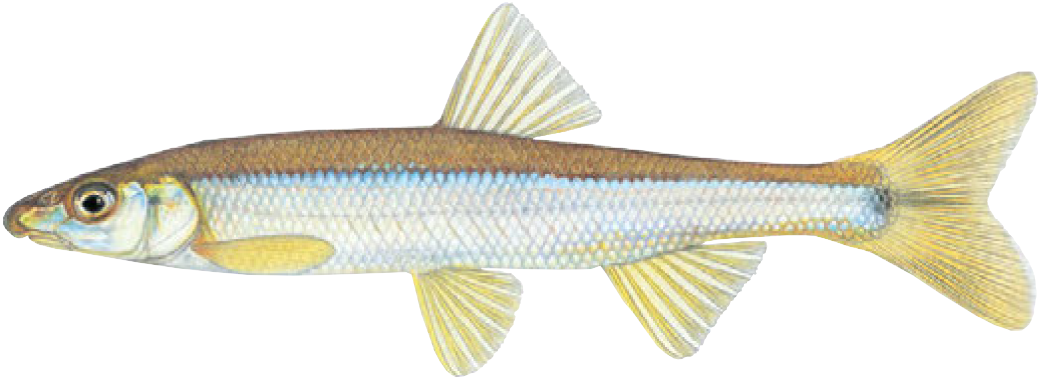


Plate 12.38. Spotfin Chub, *Erimonax monachus*

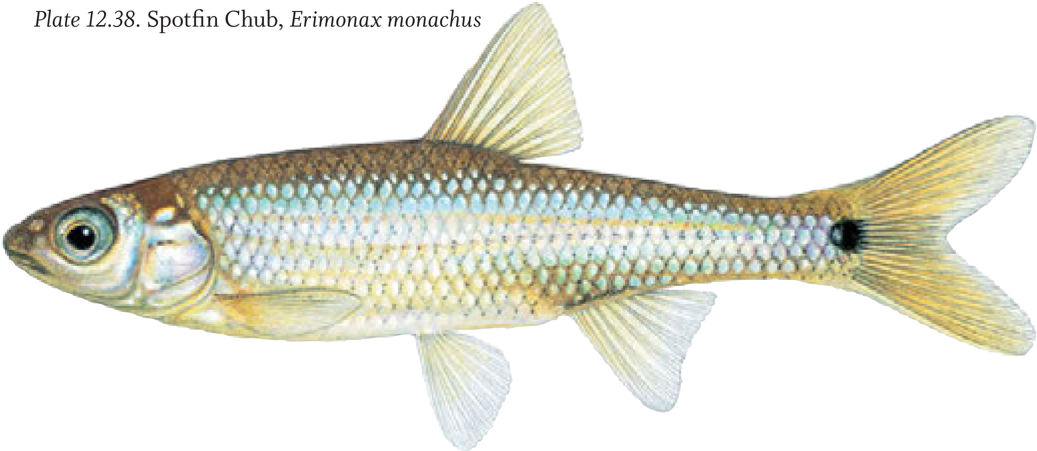


Plate 12.39. Spottail Shiner, *Hudsonius hudsonius*

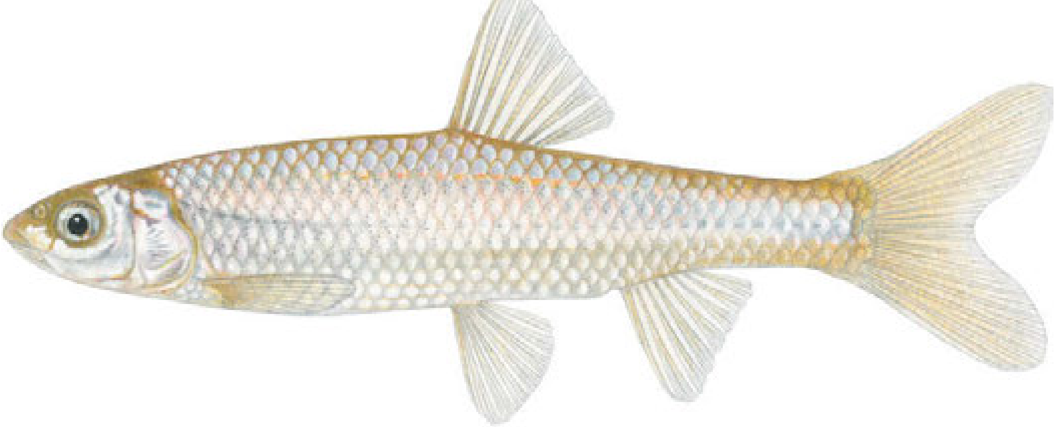


Plate 12.40. Rio Grande Silvery Minnow, *Hybognathus amarus*

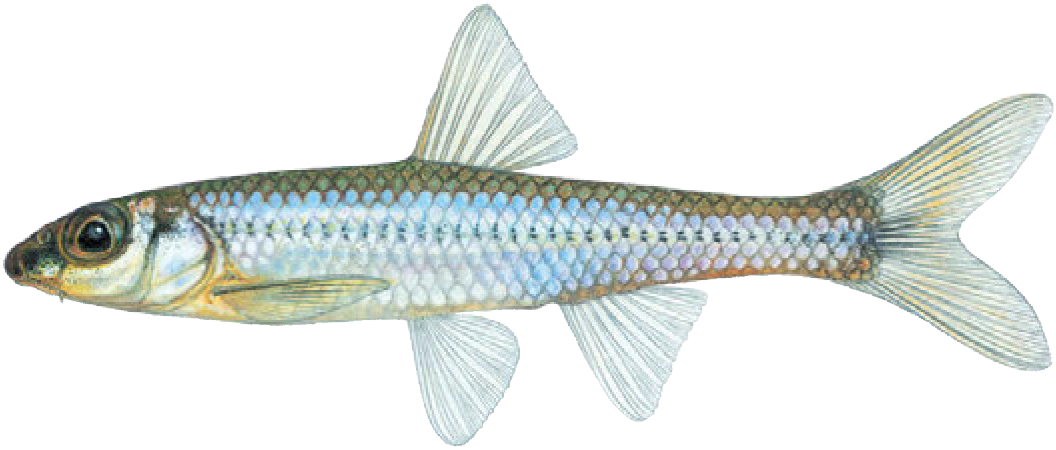


Plate 12.41. Bigeye Chub, *Hybopsis amblops*

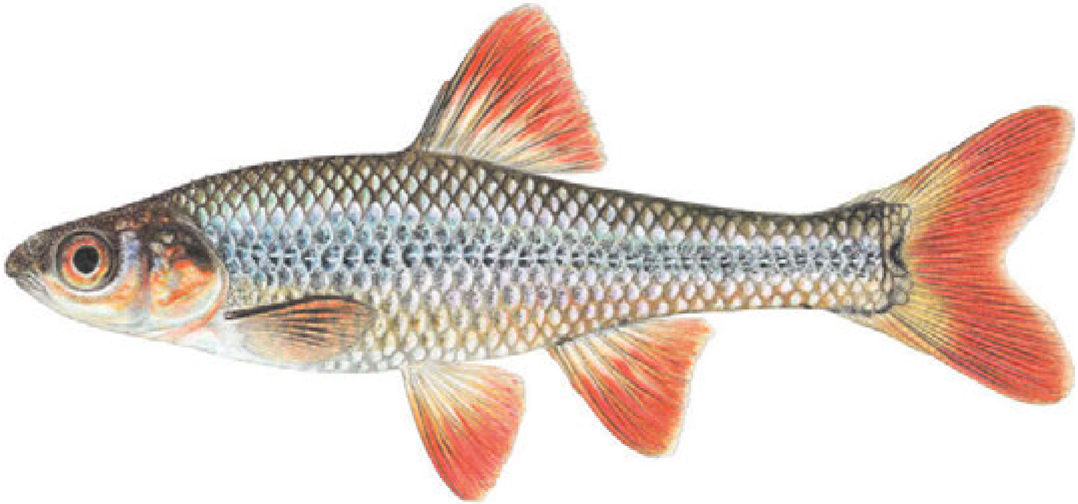


Plate 12.42. Topeka Shiner, *Miniellus topeka*

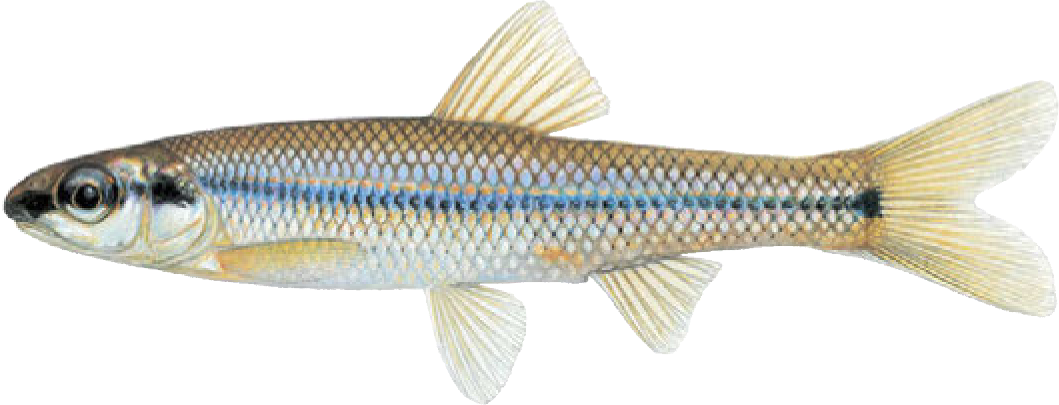


Plate 12.43. Bluntnose Minnow, *Pimephales notatus*

(see previous paragraph). A study using both mitochondrial (cytochrome *b*) and nuclear (Rag1) genes that included all species of *Cyprinella* (Schönhuth & Mayden 2010) painted a complex picture. Although recovered topologies differed somewhat for the two genes, both data sets demonstrated that the Thicklip Chub and Santee Chub should be included in *Cyprinella*. Interestingly, the genera *Codoma* and *Tampichthys* rendered *Cyprinella* paraphyletic in these analyses (Fig. 12.61).

The genus *Alburnops* contains taxa formerly included in the subgenus *Alburnops*, subgenus *Hydrophlox*, and *texanus* species group (sensu Swift 1970). Mayden et al. (2006) described the monophyly of and relationships in *Alburnops*. Cashner et al. (2011) redefined the subgenus *Hydrophlox* to include only five species.

The genus *Ericymba* is morphologically distinctive with large cephalic canals (see morphology section) and has been placed in *Notropis* and *Hybopsis* as well as *Ericymba*. *Ericymba* was part of an unresolved polychotomy at the base of the *Hybopsis* clade in Mayden's (1989) analysis. Coburn & Cavender (1992) included *Ericymba* in *Notropis* but commented on its morphological similarity to the *Hybopsis* group (also included in *Notropis* by Coburn & Cavender 1992). Raley & Wood (2001) examined cytochrome *b* sequences and included the Silverjaw Minnow, *Ericymba buccata*, in *Notropis* based on a close relationship with the "*Notropis*" *dorsalis* species group. In Simons et al. (2003), the position of *Ericymba* was unstable and analysis dependent. Using cytochrome *b*, Schönhuth & Mayden (2010) found a sister-group relationship with the clade *Aztecula* + *Yuriria* + *Graodus* (Fig. 12.61a), but analysis using Rag1 placed *Ericymba* sister to the Striped Shiner, *Luxilus chrysocephalus* (Fig. 12.61b). Mayden et al. (2006) recovered a relationship with the Silver Shiner, "*Notropis*" *photogenis*, and the Telescope Shiner, "*Notropis*" *telescopus* (Fig. 12.62). Here, we recognize the genus *Ericymba*, awaiting a more in-depth analysis of relationships in the shiner clade.

The genus *Erimonax* (Fig. 12.56a) has a complex taxonomic history, having been included in *Hybopsis*, *Erimystax*, and *Cyprinella*. Classified in *Erimystax* based on the stellate morphology of the barbel as well as other morphological characters (Mayden 1989), it was subsequently included in *Cyprinella* based on osteology and scale morphology (Coburn & Cavender 1992), biochemical data (Dimmick 1993), and spawning behavior (Jenkins & Burkhead 1994). In Simons et al. (2003) and Schönhuth & Mayden (2010), the phylogenetic position was unstable and dependent on the data set and analysis, but *Erimonax* was never recovered as a close relative of *Cyprinella* (Fig. 12.61ab). We concur with Mayden et al.'s (1992) resurrection of *Erimonax* (Jordan 1924); this is supported by several analyses (i.e., Simons et al. 2003; Bufalino & Mayden 2010ab; Schönhuth & Mayden 2010).

The genus *Hudsonius* contains three species: Spottail Shiner, *Hudsonius hudsonius*; Highfin Shiner, *Hudsonius altipinnis*; and Dusky Shiner, *Hudsonius cummingsae* (Mayden et al. 2006). Mayden et al. (2006) discussed relationships in this group and noted that the apparent paraphyly of the Highfin Shiner may indicate cryptic diversity within this species, a point alluded to by Hubbs & Raney (1948), who identified six subspecies within the species.

The genus *Hybognathus*, considered a member of the chub clade by Mayden (1989), was placed in a polychotomy with *Exoglossum* and the *Campostoma* clade (genera *Nocomis*, *Campostoma* + *Dionda*). Coburn & Cavender (1992) included *Hybognathus* in their chub clade, sister to *Dionda* + *Campostoma*. Mayden et al. (1992) considered *Hybognathus* sister to *Dionda* + *Campostoma*. Schmidt (1994) examined phylogenetic relationships of species in this genus. Simons et al. (2003) included *Hybognathus* in the shiner clade but could not identify the sister-taxon of this clade. Schönhuth et al. (2008) identified *Hybognathus* plus an undescribed species (*Dionda* sp. cf. *ipni* from Rio Axtla, San Luis Potosi, Mexico) as the sister to *Cyprinella* + *Codoma* and *Tampichthys* supporting membership of *Hybognathus* in the shiner clade (Fig. 12.60). In Schönhuth & Mayden (2010), phylogenetic positions differed for *Hybognathus* depending on the gene used in the analysis (Fig. 12.62ab). The taxon sampling and data used in these studies are insufficient to determine the phylogenetic position of *Hybognathus* with confidence.

Bailey (1951) dramatically expanded the genus *Hybopsis* to include all North American cyprinids with a terminal maxillary barbel. The taxa *Nocomis* and *Couesius* were elevated subsequently to generic status (Lachner & Jenkins 1967; McPhail & Lindsey 1970; Jenkins & Lachner 1971). Mayden (1989) restricted the genus *Hybopsis* to the subgenus *Hybopsis*; the *dorsalis* species group; the Thicklip Chub, *Cyprinella labrosa*; Santee Chub, *C. zanema*; Balsas Shiner, *Graodus boucardi*; Yellow Shiner, *Aztecula calientis*; Whitemouth Shiner, *"Notropis" alborus*; and Bridle Shiner, *"Notropis" bifrenatus*. Several of these taxa have since been removed from *Hybopsis*. Shaw et al. (1995) and Grose & Wiley (2002) examined relationships of the *H. amblops* species group. We restrict *Hybopsis* to five species (as in Mayden et al. 2006): Bigeye Chub, *H. amblops*; Highback Chub, *Hybopsis hypsinotus*; Lined Chub, *Hybopsis lineapunctatus*; Rosyface Chub, *H. rubrifrons*; and Clear Chub, *Hybopsis winchelli*.

The genus *Luxilus* was removed from synonymy with *Notropis* by Mayden (1989). Mayden considered *Luxilus* as the sister to *Cyprinella*. Coburn & Cavender (1992) considered *Luxilus* sister to a clade containing the genera *Lythrurus*, *Cyprinella*, *Pimephales*, and *Opsopoeodus*. Mayden (1989) identified three characters supporting monophyly of *Luxilus*, including retrorse preorbital tubercles, cleithral region with intense pigmentation, and epibranchial 3 with an elongate and curled uncinate process. Interspecific relationships were examined using morphology (Gilbert 1964), biochemical data (Buth 1979a), and DNA sequences (Dowling & Naylor 1997). Gilbert (1964) recognized three species groups: the *L. coccogenis* group, the *L. zonatus* group (Fig.12.56h), and the *L. cornutus* group. He noted that significant morphological breaks occurred between each group and that they did not appear closely related to one another. Buth (1979) also identified three species groups but argued that the Crescent Shiner, *Luxilus cerasinus*, was not part of the *L. cornutus* group and should be considered a separate lineage. Dowling & Naylor (1997) also recovered three species groups, but bootstrap support was low for relationships among these groups and the Crescent Shiner. Mayden et al. (2006) identified four species groups but found no evidence that *Luxilus* is monophyletic (Fig. 12.62). Schönhuth & Mayden (2010) found support for a sister-group relationship between the *L. zonatus* and *L. chrysocephalus* groups, but the Warpaint Shiner, *Luxilus coccogenis*, was recovered as sister to the Ghost Shiner, *Notropis buchanani*, rather than other *Luxilus* (Fig. 12.61a). Additional work is needed to determine the extent, membership, and relationships of *Luxilus*.

Mayden (1989) considered the genus *Lythrurus* sister to *Luxilus* + *Cyprinella*. Coburn & Cavender (1992) placed

Lythrurus as sister to a clade containing the genera *Cyprinella*, *Pimephales*, and *Opsopoeodus*. Molecular analyses do not provide a clear picture of the phylogenetic position of this genus (Figs. 12.61 and 12.62). Schmidt et al. (1998) examined interspecific relationships in *Lythrurus* based on DNA sequences of the mitochondrial cytochrome *b* gene.

The genus *Miniellus* is a monophyletic group containing the Blackchin Shiner, *Miniellus heterodon*; Sand Shiner, *Miniellus stramineus*; Topeka Shiner, *Miniellus topeka*; and Swallowtail Shiner, *Miniellus procne*. Mayden (1989) and Schmidt & Gold (1995) recognized a group containing the Sand Shiner, Topeka Shiner, and Swallowtail Shiner using morphology and cytochrome *b* sequences, respectively. Mayden et al. (2006) added the Blackchin Shiner to this group and recommended that the group be removed from synonymy with *Notropis*.

Bailey (1951) placed nearly all non-barbelled shiners (except *Hybognathus* and *Pimephales*) in the genus *Notropis*. Here, we restrict the genus *Notropis* to the former subgenus *Notropis* (see Bielawski & Gold 2001) and a number of species of uncertain relationship ("*Notropis*" of Mayden et al. 2006). Bielawski & Gold (2001) resolved interspecific relationships in the subgenus *Notropis*. Wood et al. (2002) and Berendzen et al. (2008) examined relationships and species boundaries in the *N. rubellus* species group, presenting evidence for undescribed diversity.

The genus *Pimephales* has long been considered a close relative of the Pugnose Shiner, *Opsopoeodus emiliae*, based on morphology (Coburn & Cavender 1992), reproductive behavior (Page & Johnston 1990a), and molecular data (Simons et al. 2003). Schmidt et al. (1994) and Bielawski et al. (2002) examined phylogenetic relationships of *Pimephales*; however, their analyses may be compromised by outgroup choice. Both studies used the Pugnose Shiner as the outgroup, making the assumption that *Pimephales* was monophyletic. Larger-scale molecular phylogenetic analyses that have included species of *Pimephales* and the Pugnose Shiner suggest that *Pimephales* is paraphyletic with respect to the Pugnose Shiner (Mayden 2002; Simons et al. 2003; Mayden et al. 2006; Schönhuth & Mayden 2008); however, support values for these relationships are weak. Pugnose Shiners exhibit a suite of morphological characters that distinguish them from *Pimephales*; thus, we continue to recognize the genus *Opsopoeodus* until these relationships are resolved.

The genus *Pteronotropis* usually is divided into two groups based on overall morphological similarity. The Broadstripe Shiner, *Pteronotropis euryzonus*, Sailfin Shiner, *Pteronotropis hypselopterus*, Orangetail Shiner, *Pteronotropis merlini*, and Flagfin Shiner, *Pteronotropis signipinnis*, for example, are relatively deep-bodied fishes with a prominent, dark, wide, lateral band; nuptial males have bright orange, red, and blue colors on the body and fins and develop enlarged dorsal and anals fins. The Bluehead Shiner, *Pteronotropis hubbsi*, and Bluenose Shiner, *Pteronotropis welaka*, are more terete than other members of the genus, but the nuptial males develop dramatically enlarged dorsal, anal, and pelvic fins as well as an intense blue color on the head or snout (Fig. 12.56f). Phylogenetic analyses of this group have produced conflicting results with little evidence for monophyly of the group. Dimmick (1987) found evidence for a monophyletic group containing the Flagfin Shiner, Sailfin Shiner, and Bluenose Shiner, based on allozyme electrophoresis of 21 gene loci. His analysis did not provide evidence of a close relationship of the Bluehead Shiner with these taxa. Mayden (1989) recognized four species in *Pteronotropis*, but placed the Bluehead Shiner in *Notropis*. Simons et al. (2000) examined relationships among species of *Pteronotropis* using DNA sequences of the mitochondrial cytochrome *b* gene. Outgroup taxa were included to represent taxa previously proposed as close relatives of *Pteronotropis*. They recovered two monophyletic groups, the first contained the Bluehead Shiner, Flagfin Shiner, and Bluenose Shiner, and the second contained the Broadstripe Shiner and Sailfin Shiner. Simons et al. (2000) found no evidence that these two clades formed a monophyletic group. Interestingly, in a larger-scale analysis of representatives of nearly all North American cyprinid genera, Simons et al. (2003) consistently recovered the Bluehead Shiner and Broadstripe Shiner as sister-taxa. Unfortunately, these were the only putative *Pteronotropis* included in their study. Mayden et al. (2006) included six species of *Pteronotropis* in their analysis and, similar to previous studies, did not recover a monophyletic *Pteronotropis*. The Broadstripe Shiner, Sailfin Shiner, and Flagfin Shiner formed a monophyletic group, but no evidence existed for a sister-taxon relationship with the other group of *Pteronotropis* consisting of the Redeye Chub, *Pteronotropis harperi* (not formerly considered part of the *Pteronotropis* group), Bluehead Shiner, and Bluenose Shiner.

The phylogenetic positions of *Evarra* and *Stypodon* are unclear. Both genera are extinct, and little is known of their morphology.

The North American cyprinid fauna is not monophyletic. Less clear is the number of monophyletic North American clades of cyprinids. As noted, North American cyprinids contain representatives of two major cyprinid clades: phoxinins and leuciscins (Cavender & Coburn 1992). Phoxinins are Laurasian in distribution and may have representatives southward into China. Leuciscins, in contrast, are confined to North America and Europe. The lone leuciscin native to North America is the Golden Shiner, *Notemigonus crysoleucas*, which is related to European cyprinids, specifically the genera *Abramis*, *Blicca*, *Chondrostoma*, *Leuciscus*, and *Scardinius* (Briolay et al. 1998; Cunha et al. 2002). Bailey (1951) placed the North American genus *Pfrille* into synonymy with *Chrosomus*. Banarescu (1964) then placed *Chrosomus* into synonymy with *Phoxinus*, thus creating the only cyprinid genus containing both Eurasian and North American species. This change was based on the remarkable similarity of *Pfrille* and *Chrosomus* to the Eurasian Minnow, *Phoxinus phoxinus*. Chen (1994) hypothesized that the genus *Phoxinus* was monophyletic and sister to a clade of Asian phoxinins including the genera *Eupallasella*, *Lagowskiella*, and *Rhynchocypris*. Chen suggested that *Phoxinus* and the *Eupalasella* clade were sister to a clade containing *Margariscus*, *Couesius*, and *Semotilus*. Simons & Mayden (1998) presented evidence that North American species of *Phoxinus* were sister to the western clade. They suggested that if *Phoxinus* was truly the sister to the western clade, the creek chub + plagopterin clade and the OPM clade would have Asian representatives or would compose the sister group to an Asian taxon. This prediction was partially supported by Strange & Mayden (2009), who identified the Asian genus *Rhynchocypris* as sister to a clade containing *Hemitremia*, *Semotilus*, *Couesius*, and *Margariscus* (plagopterins were not included in their analysis). Strange & Mayden (2009) also clarified the paraphyly of *Phoxinus* (sensu Banarescu) and recommended that the North American taxa be removed from synonymy with *Phoxinus* and assigned to *Chrosomus*. Howes (1984) proposed another transcontinental relationship suggesting a sister-group relationship between *Pogonichthys* and *Tribolodon*. The genus *Pogonichthys* is native to the Sacramento River system, California, and the genus *Tribolodon* is native to Japan, China, and Korea. Coburn & Cavender (1992) disagreed with Howes, placing *Pogonichthys* in their western clade. Coburn & Cavender (1992) did consider *Tribolodon* closely related to the North American fauna; *Tribolodon* and *Rhynchocypris* were resolved as part of their Chub clade. Simons & Mayden (1999) described evidence for considering *Pogonichthys* sister to *Mylocheilus*, native to Pacific drainages from the Columbia River north to the Nass River, British Columbia. They cited genetic data as well as a shared tolerance of brackish water, unusual in cyprinids. Simons & Mayden (1999) speculated that *Pogonichthys* and *Mylocheilus* were related closely to *Tribolodon* based on tolerance of brackish water and similar male nuptial coloration. Resolution of the relationships of the North American cyprinid fauna, both identifying relationships of the native genera and species and determining the relationship of the fauna with that of other continents, will require substantial taxon sampling and large-scale analyses with the inclusion of multiple loci.

FOSSIL RECORD

The history of North American cyprinid paleoichthyology extends from Cope's work in the late 1800s to the present day. Early work was primarily descriptive, defining new species, specimens, or the composition of faunas from a geological formation. More contemporary integrative approaches used the cyprinid fossil record to examine faunal changes and rates of diversification (G. R. Smith 1981; Smith et al. 2002).

The North American cyprinid fossil record is limited to the Middle Cenozoic with most fossils described from Pliocene (5.3–1.8 mya) and Pleistocene (1.8 mya to 10,000 years ago) localities (Fig. 12.63; reviewed by G. R. Smith 1981). The oldest fossils, all of which represent extinct taxa, are from the Oligocene (34–32 mya) of northwestern North America. Other fossils indicate that most cyprinid trophic guilds were already in place by the end of the Oligocene (Cavender 1991). Sadly, many of these Oligocene cyprinids are not formally described.

Fossil cyprinids from the Miocene (23–5.3 mya) are much better known than those of the Oligocene and include representatives from seven extant genera (*Acrocheilus*, *Gila*, *Mylocheilus*, *Mylopharodon*, *Notropis*, *Orthodon*, and *Ptychocheilus*) and one extinct genus (†*Idadon*; G. R. Smith 1981). Fossil localities are widespread and include western Montana (Cavender 1991); Sentinel Butte, North Dakota (Cavender 1991); Kansas (G. R. Smith 1981); and Oregon (Kimmel 1975). These taxa with representatives from the western clade and the OPM clade (Simons & Mayden 1999) indicate that much of the diversity of the North American cyprinid fauna had evolved by the Miocene (about 23–5.3 mya). A wide range of trophic morphologies occurs in Miocene cyprinids. Inferences based on tooth morphology suggest this fauna included carnivorous, herbivorous, and molluskivorous cyprinids (Kimmel 1975).

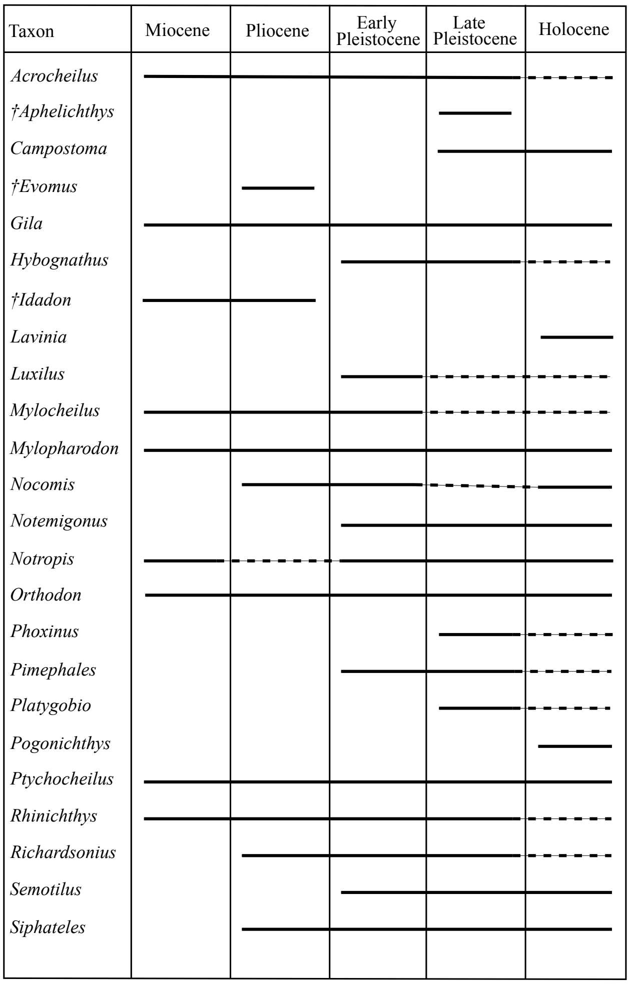


Figure 12.63. Fossil record of North American cyprinid genera. Solid line indicates the presence of fossils and dashed line indicates inferred presence based on previous fossil data.

The best known locality for North American fossil cyprinids is Lake Idaho. This locality was studied sporadically since Cope (1870) first described the fauna and contains both Miocene (23–5.3 mya) and Pliocene (5.3–1.8 mya) deposits (Kimmel 1975; Smith 1975). Uyeno (1961a) detailed the fauna of Pliocene Lake Idaho, describing a new species of cyprinid and revising the generic assignments of Cenozoic North American fishes. Smith (1975) reviewed and described the fishes of the Pliocene Glenns Ferry Formation, part of fossil Lake Idaho. This lake was large and stable for 4–10 million years before its capture by the Columbia River system. The Glenns Ferry Formation contained about 30 species, including ≥10 cyprinids. The cyprinid fauna was trophically diverse, as inferred by pharyngeal tooth morphology with several specialized forms, including †*Ptychocheilus arciferus*, a large piscivore; †*Acrocheilus latus* and †*Orthodon hadrognathus*, presumably algivores; and †*Mylocheilus robustus* and †*M. inflexus*, presumed molluskivores. Extant species from genera that were members of the Lake Idaho fossil fauna are not as specialized as the extinct forms (Smith 1975). Thus the fossil fauna of Lake Idaho is similar to that of other lacustrine systems in which closely related sympatric taxa develop specialized trophic morphologies (Greenwood 1984; Smith & Todd 1984; Nagelkerke et al. 1994).

The North American cyprinid fossil record increases in the Pliocene and Pleistocene (1.8 mya to 10,000 years ago) but is still relatively poor (Fig. 12.63). Most fossils are from lacustrine environments, and this could bias the represented diversity because most contemporary cyprinid diversity exists in streams and rivers, habitats less amenable to fossil preservation or discovery. The fossil record of pre-Pleistocene cyprinids is dominated by western North American genera, including *Gila*, †*Idadon*, *Mylocheilus*, *Mylopharodon*, *Orthodon*, *Ptychocheilus*, and *Siphateles* (G. R. Smith 1981). This also points to bias in preservation as most of the extant diversity of North American cyprinids is present in the Mississippi River basin. The cyprinid fossil record also may be biased because the bones of these fishes are small and delicate and may be missed in excavations or misidentified in museums. Most cyprinid fossils from Pliocene and Pleistocene localities represent extant genera, if not species (Uyeno & Miller 1963; G. R. Smith 1981). The fossil evidence of a paucity in large-scale taxonomic changes in cyprinids over the past 5 million years is corroborated by molecular evidence (Dowling et al. 2002; Simons 2004; Berendzen et al. 2008b). Interestingly, cyprinid fossils show similar diversity throughout the past 2 million years, which could indicate that the Pleistocene mammalian megafaunal extinctions were not mirrored in cyprinids (Gobalet & Fenenga 1993).

Diversification of North American cyprinids is likely much older than generally recognized. The fossil record of Great Basin cyprinids, together with examination of molecular phylogenies (see phylogenetic relationships section) indicates that the divergence between major cyprinid lineages had occurred by the Miocene. Genetic divergence between allopatric taxa was often older than the most recent geographic connection between the drainages the taxa inhabit (Smith et al. 2002). Thus, the most recent biogeographic event may not be the event responsible for the initial vicariance, and historical inferences based only on extant taxa may be misleading because of a tendency to consider the most recent events as responsible for diversity (G. R. Smith 1981). Clearly, an accurate assessment of biogeographic history requires well-supported phylogenies and molecular clocks well calibrated against the fossil record.

MORPHOLOGY

Cyprinids, despite their huge diversity, maintain a relatively conserved overall body plan. A single dorsal fin, whose anterior-most ray may be enlarged and stiff, usually sits midway along the body. The pelvic fins are also typically midway along the body, and an anal fin slightly smaller than the dorsal sits between the pelvic fins and the caudal fin. The caudal fin of most cyprinids is wide-lobed with rounded edges, erupting from a caudal peduncle larger than typical of most other groups of fishes. Mouth position ranges from inferior to terminal. All species have cycloid scales, although these are sometimes minute and embedded in the skin, and many have a silvery appearance. A lateral-line canal can be seen on the flanks of most species, and sometimes the sensory canals are expanded on the head. Because of so many conserved features, cyprinids often are considered to be morphologically monotonous, a misconception that has impeded the understanding of the functional and evolutionary biology of these organisms.

Most North American cyprinids are small (<15 cm), and some are <50 mm as adults.The Ornate Shiner, *C. ornata*, is <58 mm SL and the Blackstripe Minnow, *Tampichthys rasconis*, has a maximum recorded size of 53 mm SL (Miller et al. 2005). In contrast, some species are large, achieving sizes of >1 m TL; the largest North American cyprinid, the Colorado Pikeminnow, *P. lucius*, is reputed to reach 1.8 m TL (Moyle 2002). The maximum recorded age also varies substantially from as few as 2 years in the Pugnose Shiner, *Opsopoeodus emiliae* (otolith samples; Becker 1983), and Kanawha Minnow, *Phenacobius teretulus* (length frequency data; Jenkins & Burkhead 1994), to 42 years in the Bonytail Chub, *Gila elegans* (otolith samples; Rinne et al. 1986).

We begin our review of cyprinid morphology by considering in detail three aspects of cyprinid morphology with the greatest diversity and functional significance: trophic morphology, sensory structures, and nuptial structures. We conclude our exploration of cyprinid morphology with a description of the application of this diversity to taxonomy and ecology; this final subsection includes a synthesis of general trends emerging in ecomorphological literature. Additional descriptions and discussions of morphology can be found in phylogenetic and systematic literature. Harrington (1955) provided a detailed description of the cranial osteology of the Bridle Shiner, *"Notropis" bifrenatus*. Uyeno (1961b) described the osteology of *Gila* and other western genera, and this work remains the best description of osteology of Pacific Slope cyprinids. Mahy provided detailed descriptions of the cranial (1975a) and axial (1975b) skeletons of the Finescale Dace, *Chrosomus neogaeus*, followed by comparisons with other species in the genus (Mahy 1975c). Barbour & Miller (1978) described aspects of the osteology of the Mexican genus *Algansea*. Mayden (1989) provided detailed descriptions of osteological characters of North American cyprinids with emphasis on the genus *Cyprinella*. Coburn &Cavender (1992) used osteological and scale characters to investigate relationships of all North American cyprinid genera. These papers should provide the interested reader with a sound background in osteology and morphology of the North American Cyprinidae.

Trophic Morphology

Trophic structures include the jaws, buccal cavity, pharynx, and gut. Unsurprisingly, variation in these morphologies is correlated with diet (see ecology section for a discussion of difficulties characterizing cyprinid diets). Cyprinids, like all cypriniform fishes, have a unique method of jaw protrusion mediated by the kinethmoid (Fig. 12.64), a sesamoid bone, derived from an ossified ligament (Conway et al. 2010). The kinethmoid links, via ligaments, the ethmoid complex, the maxilla, the palatine, and the premaxilla. Though it is a simple cylindrical shape in some species, the diversity in shape of the kinethmoid is astounding, and this diversity may be functional in trophic radiation (Hernandez et al. 2007). During jaw protrusion, the kinethmoid rotates, allowing extension of the premaxilla away from the cranium (Alexander 1966), though the specific mechanics of protrusion are still being investigated. Jaw protrusion likely aids in suction performance in these fishes by orienting suction flow toward the food item and enlarging the volume of the buccal cavity.

Jaw morphology is variable among North American cyprinids and is a function of diet. Piscivores, such as *Ptychocheilus* and *Semotilus*, have large terminal mouths. Insectivores have smaller mouths and the orientation and position of the mouth varies. Species that feed on drift or

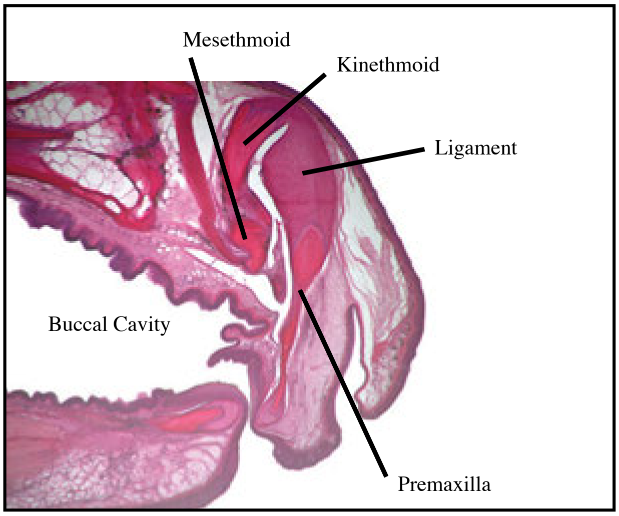


Figure 12.64. Parasaggital section of Suckermouth Minnow, *Phenacobius mirabilis*, illustrating kinethmoid bone and associated elements.

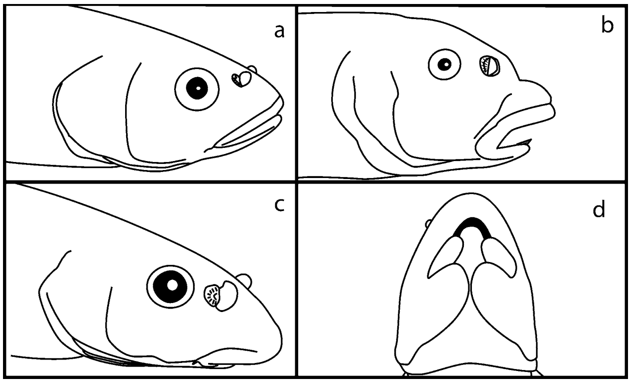


Figure 12.65. Mouth shapes of some example taxa: (a) Creek Chub, *Semotilus atromaculatus* JFBM 40199, a piscivore, demonstrating a terminal mouth; (b) Central Stoneroller, *Campostoma anomalum*, an algivore, demonstrating the algae scraper on the lower jaw (shaded in gray); (c) Longnose Dace, *Rhinichthys cataractae* JFBM 17515, demonstrating an inferior mouth position; (d) Cutlips Minnow, *Exoglossum maxillingua* JFBM 30194, demonstrating tri-lobed lower jaw. JFBM = J. F. Bell Museum of Natural History.

at the surface have terminal mouths (Fig. 12.65a); examples include the Emerald Shiner, *Notropis atherinoides*, and Common Shiner, *Luxilus cornutus*. Species that feed on the substrate have subterminal or inferior mouths and may have fleshy lips with large numbers of taste buds (e.g., Stargazing Minnow, *Phenacobius uranops*; Streamline Chub, *Erimystax dissimilis*; Fig. 12.65a). Still other minnows, such as the Pugnose Minnow, *Opsopoeodus emiliae*, have slightly upturned mouths. The oral jaws of cyprinids lack teeth, but the lips are often keratinized, and the degree of keratinization is related to feeding. Algivores, such as *Campostoma* and *Acrocheilus*, scrape diatoms and other algae from the surface of rocks (Scott & Crossman 1973; Fowler & Taber 1985). This leaves characteristic bare patches on rock surfaces in the streams where these fishes occur (Matthews et al. 1986). These algivores have large, flat, keratinous surfaces on the jaws that serve as scrapers (Fig. 12.65b). Large keratinous sheaths on the jaws are known from other taxa, including the spring-dwelling Desert Dace, *Eremichthys acros* (Hubbs & Miller 1948). The two species in *Exoglossum*, the Tongue-tied Minnow, *Exoglossum laurae*, and Cutlips Minnow, *Exoglossum maxillinguae*, have highly unusual jaws (Fig. 12.65d). The lower jaw in these fishes has three lobes, but the functional significance of the lobed jaw is unclear. Diet studies indicate that both species feed on insects (Greeley 1927; Johnson 1981; Jenkins & Burkhead 1994). The Cutlips Minnow is commonly referred to as the eye biter by bait vendors; this species will scoop the eyes out of other fishes kept in the same bucket or tank (Scott & Crossman 1973; see behavior section). This behavior is undocumented in the wild, and it is unclear if this is associated with feeding or aggression.

Sorting of food particles takes place in the buccal cavity and pharynx. Mouth tasters (sensu Davis & Miller 1967) have large numbers of taste buds located in folds of the buccal cavity. Throat tasters have large numbers of taste buds in the pharynx. In throat tasters, food selection and retention is mediated by the gill rakers and the palatal organ (Sibbing 1988). The size and spacing of the gill rakers is correlated with diet (Fig. 12.66). Cyprinids that feed on relatively large food items have short, widely spaced gill rakers, but those that feed on smaller food items such as zooplankton or phytoplankton have long, closely spaced gill rakers. This phenomenon is well illustrated by the Tui Chub, *Siphateles bicolor*, from Pyramid Lake, Nevada (Snyder 1917). Two forms of this species exist in Pyramid Lake, a benthic feeder and a limnetic plankton feeder (La Rivers 1962), which are distinguished easily by gill raker counts and spacing (Snyder 1917; La Rivers 1962). The benthic feeder has short, widely spaced gill rakers and the limnetic form the opposite morphology. The Popoche Chub, *Algansea popoche*, is a benthic feeder and uses its numerous, long, thin gill rakers to filter food from mud and organic matter (Miller et al. 2005). The Sacramento Blackfish, *Orthodon microlepidotus*, is a phytoplanktivore native to the Sacramento River drainage, California (Fig. 12.43). This species is remarkable for its elongate, broomlike gill rakers that

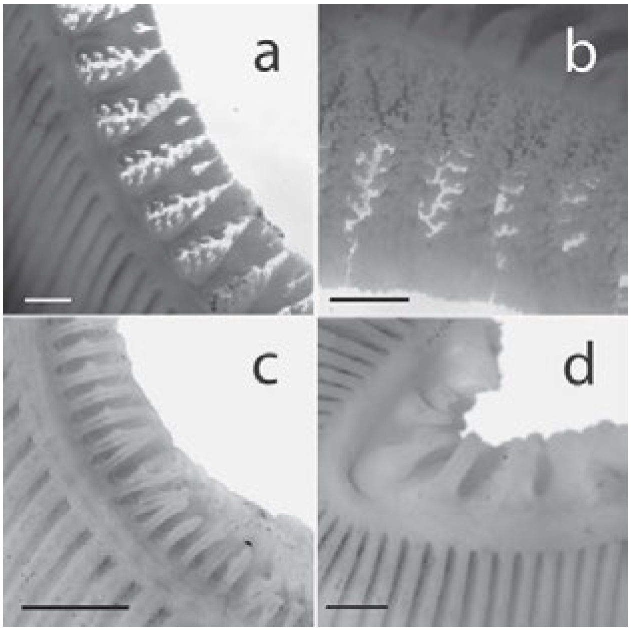


Figure 12.66. Gill rakers of selected North American cyprinids: (a) Sacramento Blackfish, *Orthodon microlepidotus* JFBM 18856, lateral view; (b) Sacramento Blackfish, *O. microlepdotus* JFBM 18856, medial view; (c) Central Stoneroller, *Campostoma anomalum* JFBM 31384, lateral view; (d) Creek Chub, *Semotilus atromaculatus* JFBM 37006, lateral view. Scale bars = 1.0 mm. JFBM = J. F. Bell Museum of Natural History.

are used to filter plankton from the water column (Moyle 2002; Fig. 12.66ab).

North American cyprinids have a palatal organ that is located in the roof of the pharynx (Fig. 12.67). This structure contains striated muscle fibers in a variety of orientations and has large numbers of taste buds on its surface (Sibbing & Uribe 1985). Sibbing (1988) hypothesized that the palatal organ can pin food particles against the gill rakers while non-food items are flushed from the pharynx. The palatal organ of *Hybognathus* is unusual among North American cyprinids in that it has large papillae on the pharyngeal surface. The arrangement of papillae is species specific, but their functional significance is unknown (Hlohowskyj et al. 1989).

One of the most striking aspects of trophic morphology in cyprinids is the presence of large, variably shaped teeth in the back of the throat. These teeth develop in surrounding epithelium and ankylose onto a highly modified and enlarged ceratobranchial V, forming the pharyngeal jaws. This is the only element of the fifth gill arch that is still present in cyprinid fishes; the other branchial elements have been lost. The ceratobranchial V varies greatly in morphology, the variations typically correlating with diet. The enlargement of the ceratobranchial V provides large surfaces for muscle attachment, and several muscle groups are associated with the ceratobranchial. The arrangement of these muscles and the ceratobranchial is analogous to the muscular sling of labroid fishes, though their function and evolution is far less understood than the labroid system. Five muscles are on each side of the jaw. The largest of these, the levator arcus branchialis V, originates in the subtemporal myodome of the cranium and inserts on the dorso-caudal face of the fifth ceratobranchial. This muscle pulls the pharyngeal teeth dorsally (detailed by Eastman 1971; Sibbing 1991ab). Almost as large is the retractor os pharyngeus inferioris that originates on the basioccipital process and inserts on the posterior margin of the ceratobranchial V. This muscle pulls the jaws posteriorly. Since the pedestal of bone that the pharyngeal teeth act against is angled anterio-dorsally, these two muscles together pull the teeth against the base of the skull (Fig. 12.68). The other three muscles of this complex system likely allow for a large range of movement of the ceratobranchials

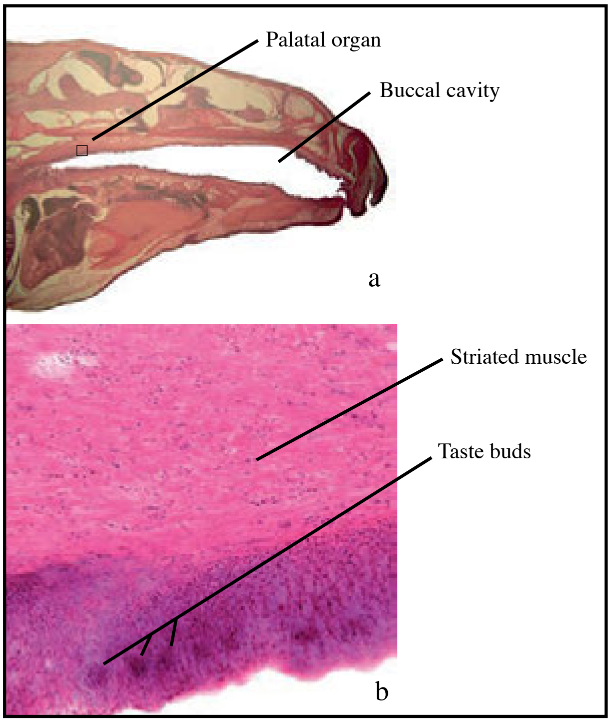


Figure 12.67. Palatal organ. (a) Parasaggital section of Suckermouth Minnow, *Phenacobius mirabilis*. (b) Detail of palatal organ. Striated muscles are loosely arranged and are covered by the pharyngeal epithelium, which contains a high density of taste buds.

with respect to each other and the cranium. In addition, contraction of the epaxial musculature moves the cranium with respect to the ceratobranchials, which may increase shearing or crushing forces (Sibbing 1991b). The muscular sling provides for complex action of the pharyngeal teeth, allowing shredding, crushing, cutting, lacerating, and shearing (Sibbing 1991b). As in labroids, the mobility of the pharyngeal jaws may be associated with the diversification of Cyprinidae. In North American cyprinids, the ceratobranchial bears one to three rows of teeth. The number of teeth, tooth rows, and the shape of the teeth are taxon specific and thus of great use in identification (e.g., Gilbert & Bailey 1972; Hubbs et al. 1974). Shape of the basioccipital varies, and this is often used to distinguish species in *Hybognathus* (Pflieger 1975). The basioccipital bears a horny pad on its surface; the makeup of this pad is unclear. It is variably referred to as collagenous (Evans & Deubler 1955) or horny (Sibbing 1982, 1991ab; Suzuki & Hibiya 1985), suggesting keratin, but to our knowledge, its histology has not been sufficiently examined.

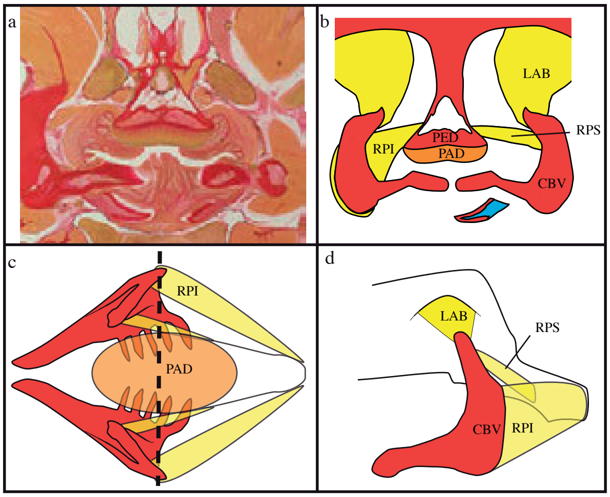


Figure 12.68. Oropharyngeal musculoskeletal anatomy of the Cyprinidae: (a) transverse section through posterior pharyngeal region of Central Stoneroller, *Campostoma anomalum*; (b) schematic of musculoskeletal anatomy in the same view; (c) dorsal view; (d) lateral view. Functional pharyngeal teeth, ankylosed to the ceratobranchial V act against a horny pad of the pharyngeal process of the basioccipital. Replacement teeth are visible in the pharyngeal epithelium (panels a and b). CBV, ceratobranchial V; LAB, levator arcus branchialus V; PAD, keratinous pad on the basioccipital; PED, basioccipital pedestal; RPI, retractor os pharyngeus inferioris; RPS, retractor os pharyngeus superioris.

Pharyngeal tooth morphology varies among cyprinid species and is correlated with diet. In piscivorous cyprinids the teeth are pointed (e.g., Creek Chub, *Semotilus atromaculatus*, Fig. 12.69). The teeth of herbivorous and detritivorous fishes such as *Campostoma*, *Hybognathus*, and Fathead Minnows, *Pimepheles promelas*, have extensive flattened surfaces (Fig. 12.69c). Shearing teeth have sharp cutting edges as well as hooked tips; these most often occur in insectivorous taxa such as *Phenacobius*. Crushing teeth are observed in molluskivores such as the Peamouth Chub, *Mylocheilus caurinus*. The Stumptooth Minnow, *Stypodon signifer*, a species now extinct, had pharyngeal teeth that were nearly spherical at their crown. These teeth were presumably used to crush the shells of snails, the remains of which are abundant in the guts of preserved specimens (Miller et al. 2005).

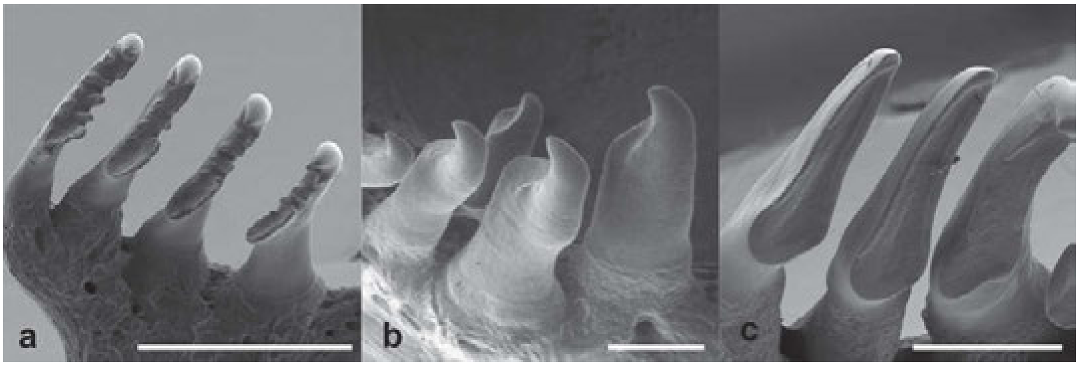


Figure 12.69. Scanning electron micrographs showing the extremes of pharyngeal arch morphology. (a) Pugnose Minnow, *Opsopoeodus emiliae*, right gill arch, dorsal view, demonstrating serrated cusp morphology. Anterior to the right. (b) Creek Chub, *Semotilus atromaculatus*, right gill arch, ventral view, demonstrating shearing tooth cusp morphology and hooked cusp tips. Anterior to the left. (c) Fathead Minnow, *Pimephales promelas*, right gill arch, dorsal view, demonstrating flattened tooth cusp morphology. Anterior to the right. Scale bars = 0.5 mm.

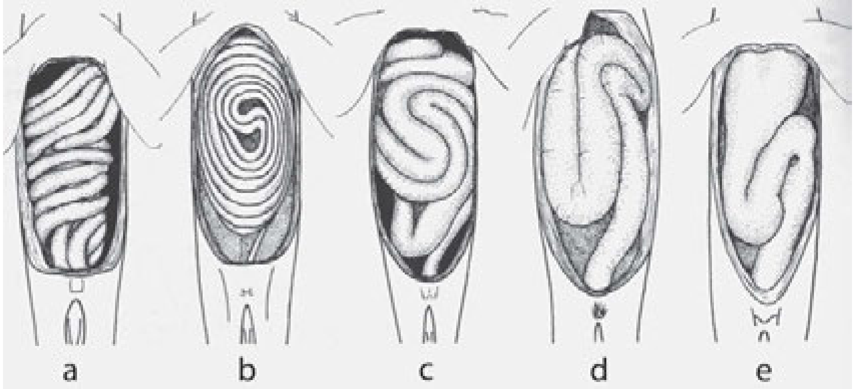


Figure 12.70. Gut length and coiling patterns: (a) *Campostoma*, (b) *Hybognathus*, (c) Bluehead Chub, *Nocomis leptocephalus*, (d) Bull Chub, *Nocomis raneyi*, (e) most minnows (redrawn from Jenkins & Burkhead 1994).

Multiple cusps occur in a number of North American taxa, giving the teeth a serrate appearance (e.g., Golden Shiner, *Notemigonus crysoleucas*; Pugnose Minnow, *Opsopoeodus emilae*; Fig. 12.69a). The functional significance of these cusp shapes is unknown. Tooth morphology may exhibit ontogenetic variation. Juvenile Peamouth Chubs have teeth that are sharp and pointed, similar to those of insectivores. The juvenile dentition is replaced by molariform teeth (Scott & Crossman 1973) and presumably accompanies a shift in diet (Aspinwall et al. 1993).

Pharyngeal teeth are replaced regularly and tooth replacement patterns are conserved across Cyprinidae (Evans & Deubler 1955; Cooper 1981; Nakajima 1987). The teeth form in the pharyngeal epithelium and subsequently ankylose to the ceratobranchial. Grinding surfaces are evident on the teeth before they ankylose to the ceratobranchial and become functional. Tooth replacement appears to occur regularly enough that use does not affect tooth morphology in carnivorous taxa (Evans & Deubler 1955), but wear patterns occur in taxa that crush and grind food against the basioccipital process (Sibbing 1991a).

Cyprinids lack a true stomach, defined as a structure that produces pepsin and hydrochloric acid. The anterior of the gut is expanded to form an intestinal bulb (often mistakenly referred to as the stomach) that is elastic and can expand to hold relatively large amounts of undigested material. Gut shapes vary depending on diet (Fig. 12.70). The gut of piscivorous and insectivorous taxa is S-shaped and short, rarely exceeding the body length. In omnivorous or herbivorous taxa the gut is much longer, ranging from 2–6 times the body length (Hubbs & Miller 1948; Moyle 2002). Gut-coiling patterns differ among herbivorous fishes, suggesting that herbivory has evolved multiple times in North American cyprinids. In several species of *Campostoma*, the gut is long and loops around the gas bladder, a unique conformation in North American cyprinids (Fig. 12.70a). In the Mexican Stoneroller, *Campostoma ornatum*, the gut does not loop around the gas bladder (Page & Burr 2011). Species of *Hybognathus* have a gut that is coiled in the shape of a watch spring (Fig. 12.70b), and in several species, such as the Mountain Chub, *Algansea monticola*, gut coils run up and down the length of the abdominal cavity (Barbour & Miller 1978). Also associated with herbivory is a darkened peritoneum, although the functional significance of this is unclear. The mechanical action of the pharyngeal teeth is likely inefficient at opening cell walls, and a significant proportion of ingested algal cells may pass through the gut unharmed (Prowse 1961; Prejs 1984). The darkened peritoneum may prevent intact algal cells from photosynthesizing. If photosynthesis were allowed to occur, it would produce oxygen that might alter buoyancy and could negatively affect activity of digestive enzymes or may poison cellulolytic endosymbionts. Although no cellulolytic endosymbionts are yet identified in cyprinid intestines, fermentation products, indicating the presence of microbial fermenters, occur in the guts of *Campostoma* and *Nocomis* (German et al. 2010).

Sensory Morphologies

Cyprinids have highly developed sensory systems. Unique diversity in cyprinids exists in their chemosensory abilities and the acousticolateralis system that detects sound and motion around the fish. The relative importance of these systems to particular species is reflected in their development and brain morphology. Though other modalities exist for sensing the environment (e.g., vision), we do not discuss them here because they are not particular to North American cyprinids.

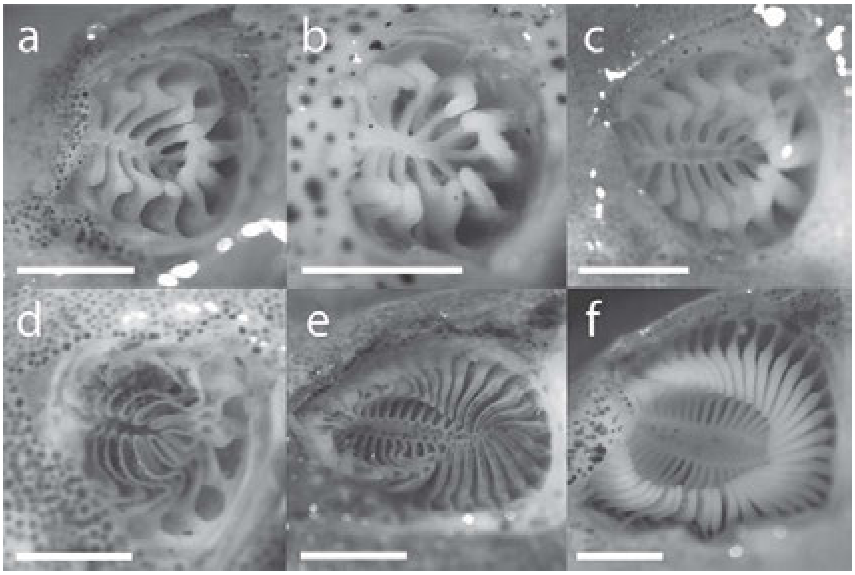


Figure 12.71. Olfactory rosettes of selected North American cyprinids (anterior to the left): (a) Yaqui Chub, *Gila purpurea* JFBM 18464; (b) Ribbon Shiner, *Lythrurus fumeus* JFBM 42291; (c) Creek Chub, *Semotilus atromaculatus* JFBM 40394; (d) Longfin Dace, *Agosia chrysogaster* JFBM 18462; (e) Blotched Chub, *Erimystax insignis* JFBM 42872; (f) Silver Chub, *Macryhybopsis storeriana* JFBM 38411. Scale bars = 1.0 mm. JFBM = J. F. Bell Museum of Natural History.

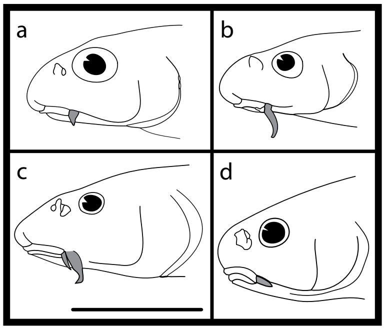


Figure 12.72. Barbel diversity in the North American cyprinid genus *Macrhybopsis*: (a) Speckled Chub, *M. aestivalis*; (b) Speckled Chub, *M. aestivalis*; (c) Peppered Chub, *M. tetranema*; (d) Sicklefin Chub, *M. meeki* (redrawn from Moore 1950).

Chemosensory systems include olfaction and taste. Olfaction is clearly important for feeding as well as social communication (Sorensen & Caprio 1998). The olfactory epithelia are arranged in a rosette-shaped structure. The size and number of the olfactory lamellae varies, but this is unquantified (NJG & AMS pers. obs.; Fig. 12.71). Cutaneous taste buds (on the external surface), present in many species of fishes including cyprinids, are particularly numerous in three genera of North American cyprinids: *Erimystax*, *Macrhybopsis*, and *Platygobio*. Taste buds are present on the barbels, first and second interradial pectoral fin membranes, and the epidermis (Moore 1950). The density of the taste buds decreases posteriorly. In *Macrhybopsis*, the taste buds can be so numerous that they form barbel-like structures. The density of taste buds reaches an extreme in the Sturgeon Chub, *M. gelida*, where they are even present on the cornea of the eye. The increase in numbers of taste buds likely is correlated with the turbidity of the large rivers that these fish inhabit (Moore 1950). The Sturgeon Chub and Sicklefin Chub, *M. meeki*, occur in the Missouri River drainage and the Mississippi River downstream of St. Louis, Missouri (Lee et al. 1980), both highly turbid rivers. Variation in location and density of taste buds is documented in *Nocomis*. Species of *Nocomis* are thought to be visual feeders and have relatively few tastebuds on the skin and barbels. The Bluehead Chub, *Nocomis leptocephalus*, is more herbivorous in habit (Flemer & Woolcott 1966; Gatz 1979; German et al. 2010) and has more cutaneous taste buds on the snout and lips than other species in the genus (Davis & Miller 1967).

Barbels are present at the posterior end of the maxilla in several species of North American cyprinids (Fig. 12.72). Presence of these barbels was once used to justify subsuming many cyprinid genera into the genus *Hybopsis* (Bailey 1951). Barbels are recognized now as phylogenetically plastic and, as with almost any organismal characteristic, cannot be used as the sole character to justify a classification (Gilbert & Bailey 1972). Barbels exhibit both intra- and interspecific variation in length, position, number, and form (see ultrastructure review by Dimmick 1988; Fig. 12.73). The genera *Semotilus*, *Couesius*, and *Margariscus* have short, flap-like triangular barbels located just anterior to the posterior end of the maxilla in the maxillary groove (Scott & Crossman 1973). In *Semotilus* and *Margariscus*, the barbels are often absent or present only on one side. The genus *Erimystax* is notable for its stellate barbels (Moore 1950; Branson 1962; Mayden 1989; Fig. 12.73a). Most other barbelled cyprinids have barbels that are conical in shape and present at the caudal end of the maxilla. With the exception of some species of *Macrhybopsis*, all barbelled North American cyprinds have a single pair. Two pairs of barbels are present in the Peppered Chub, *M. tetranema*, and often are present in specimens from some populations of Shoal Chub, *Macrhybopsis hyostoma* (Eisenhour 1999, 2004; Fig. 12.73).

The auditory system comprises the inner ear and the external neuromasts. These have a common developmental origin and are innervated by cranial nerve VIII. The inner ear is a far-field detector and responds to sound (pressure) waves traveling through the water. The external neuromasts are near-field detectors and respond to local changes in water flow around the body of the fish.

Cyprinids, like all otophysan fishes, have a Weberian apparatus, a complex of bones and ligaments between the gas bladder and the inner ear. The bones that comprise the Weberian apparatus are modified vertebrae, neural arches, ribs, and supraneurals (Fink & Fink 1981; Coburn & Futey 1996). The ossicles directly responsible for transduction are the tripus, intercalarium, scaphium, and claustrum (Fig. 12.74). The tripus is a triangular bone, the apex of which articulates with the vertebral column. The posterior end of the tripus rests against the anterior end of the gas bladder, and the anterior end of the tripus is connected via a ligament to the intercalarium. The intercalarium is connected via a ligament to the anterior-most Weberian bones, the scaphium and claustrum. These bones are in direct contact with a posterior extension of the membranous labyrinth that contains the inner ear. The gas bladder and Weberian apparatus act as a transducer; pressure or sound waves cause the gas bladder to vibrate with respect to the rest of the fish. This mechanical action is conveyed to the inner ear by the Weberian bones and ligaments. Thus, the Weberian apparatus is believed to greatly increase the efficiency of hearing of otophysan fishes, particularly at higher frequencies. Coburn & Futey (1996) described the osteology and ontogeny of the Weberian apparatus in several species of cyprinids, including the Common Shiner, *Luxilus cornutus*, and Golden Shiner, *Notemigonus crysoleucas*, clarifying the homology of the constituent elements. They found that supraneurals are not always unpaired and hypothesized that the claustra are derived from bilaterally paired supraneural I. In contrast, Fink & Fink (1981) considered supraneurals to be unpaired median elements.

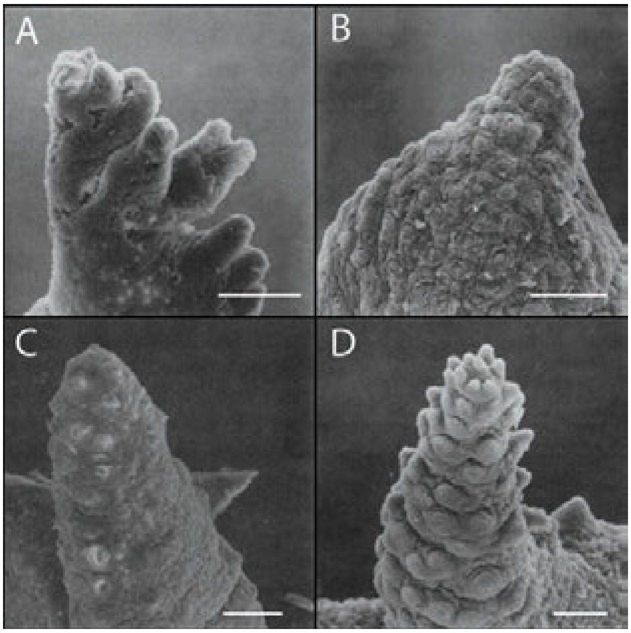


Figure 12.73. Cyprinid barbel morphology: (A) Streamline Chub, *Erimystax dissimilis*; (B) Woundfin, *Plagopterus argentissimus*; (C) Blacknose Dace, *Rhinichthys atratulus*; (D) Flathead Chub, *Platygobio gracilis*. Scale bars = 100 microns (redrawn from Dimmick 1988).

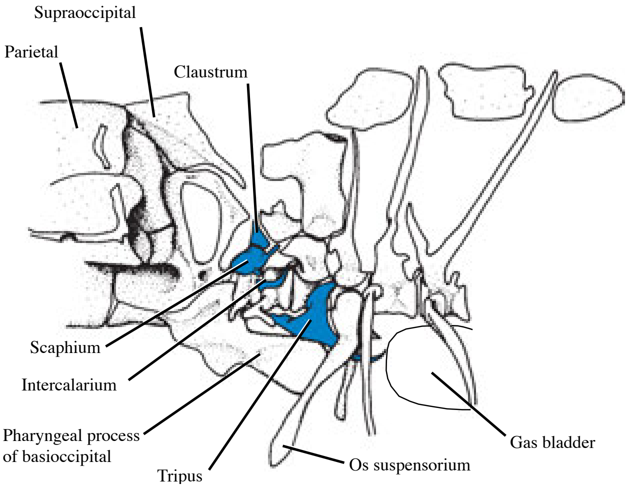


Figure 12.74. Weberian apparatus of Gibbous Shiner, *Cyprinella garmani* (redrawn from Mayden 1988).

The mechanosensory system is made up of neuromasts; these may be present on the surface of the fish or enclosed in bony canals. Most work on the comparative morphology of the lateralis system has focused on the presence or absence of various canals and connections between them. Illick (1956) described variation in the lateralis system among a wide diversity of North American cyprinids. Reno (1969) documented the lateralis system in the genera *Couesius*, *Cyprinella*, *Erimonax*, *Erimystax*, *Hybopsis*, *Macrhybopsis*, *Nocomis*, *Notropis*, *Oregonichthys*, and *Platygobio*. Species from silty streams usually have long canaliculi extending from the canals to the pores; further, the pores are relatively small, and canals are often quite long (Reno 1969). Fishes from clear streams usually have reduced or absent canaliculi and large pores. The long canaliculi and small pores presumably keep the lateralis system free of debris. Species from active or lotic environments have complete canals, but species from lentic or lentic-like systems tend to have incomplete canals (Reno 1969).

The Silverjaw Minnow, *Ericymba buccata*, and Longjaw Minnow, *E. amplamala*, have the most unusual lateralis system of any North American cyprinid. The cephalic canals are extremely large and cavernous (Fig. 12.75). The anatomy of the cephalic canals and their associated bones and the histology and distribution of the enlarged neuromasts in these canals are well described (Reno 1971; Hoyt 1972). The functional significance of these hypertrophied canals is unclear, but similar canal structure occurs in unrelated benthic feeding fishes, including the Trout-Perch (*Percopsis omiscomaycus*), Freshwater Drum (*Aplodinotus grunnniens*), and Ruffe (*Gymnocephalus cernuus*).

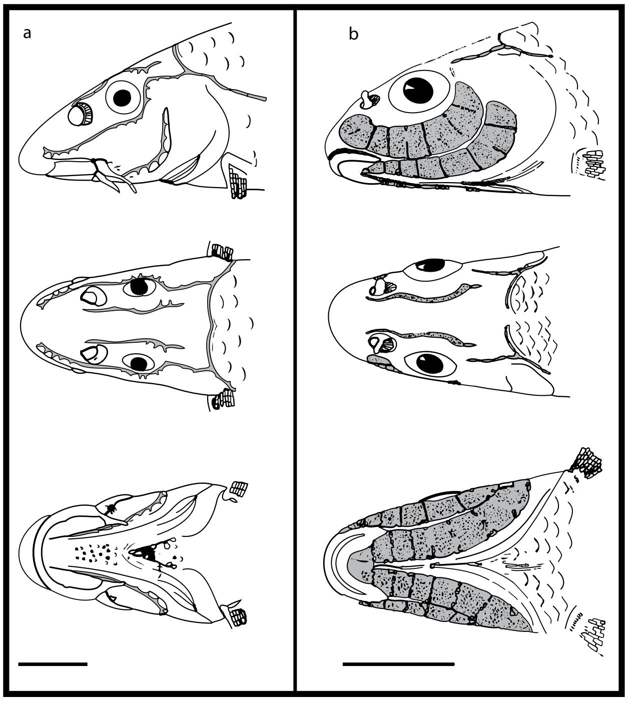


Figure 12.75. Cephalic canals in two cyprinids: (a) Speckled Chub, *Macrhybopsis aestivalis*, showing pervasive, thin canals; (b) Silverjaw Minnow, *Ericymba buccata*, showing huge and pervasive canals (redrawn from Reno 1969 and Hoyt 1972, respectively).

Nuptial Structures

Tubercles, friction pads, enlarged cephalic crests and fins, and egg-brooding pads are ephemeral structures present on the body of many cyprinids during the spawning season. Nuptial tubercles are formed from epidermal keratin (Wiley & Collette 1970). The size and location of the tubercles on the body of the fish vary among species and are often a useful taxonomic character. Nuptial structures generally appear on males but may also be present on females. Small tubercles on the fin rays and body are believed to help maintain contact between individuals during the spawning embrace (Maurakis et al. 1991a). Small tubercles also occur on the head of several species (Fig. 12.76ab); however, the function of small cranial tubercles is unknown. Scanning electron microscopy revealed seven different tubercle types in *Chrosomus* (Chen & Arratia 1996). Tubercle morphology varied with species and anatomical position. Some morphologies were specific to a single species. Other tubercle morphologies were restricted to a particular position on the fish, but some were widespread and occurred in several locations on the body.

Large tubercles, which only appear on nuptial males, occur in several taxa, including the genera *Nocomis*, *Semotilus*, *Campostoma*, *Cyprinella*, and *Pimephales* (Figs. 12.76c, 12.77, and 12.78). Large tubercles generally are located on the head, although male *Campostoma* can develop large tubercles over their entire body. All species in these genera construct or prepare nests or other spawning surfaces (see reproduction section). The males generally are territorial, defending nests from conspecifics and potential predators, and the large tubercles may be important weapons for the defense of spawning sites (Jenkins & Burkhead 1994). The pattern, size, and number of nuptial tubercles are useful systematic characters for distingishing closely related species. For example, the Hornyhead Chub, *Nocomis biguttatus*, and River Chub, *Nocomis micropogon*, are distinguished most easily by tuberculation pattern.

In addition to tubercle growth, other changes in morphology are obvious in cyprinids at the height of the

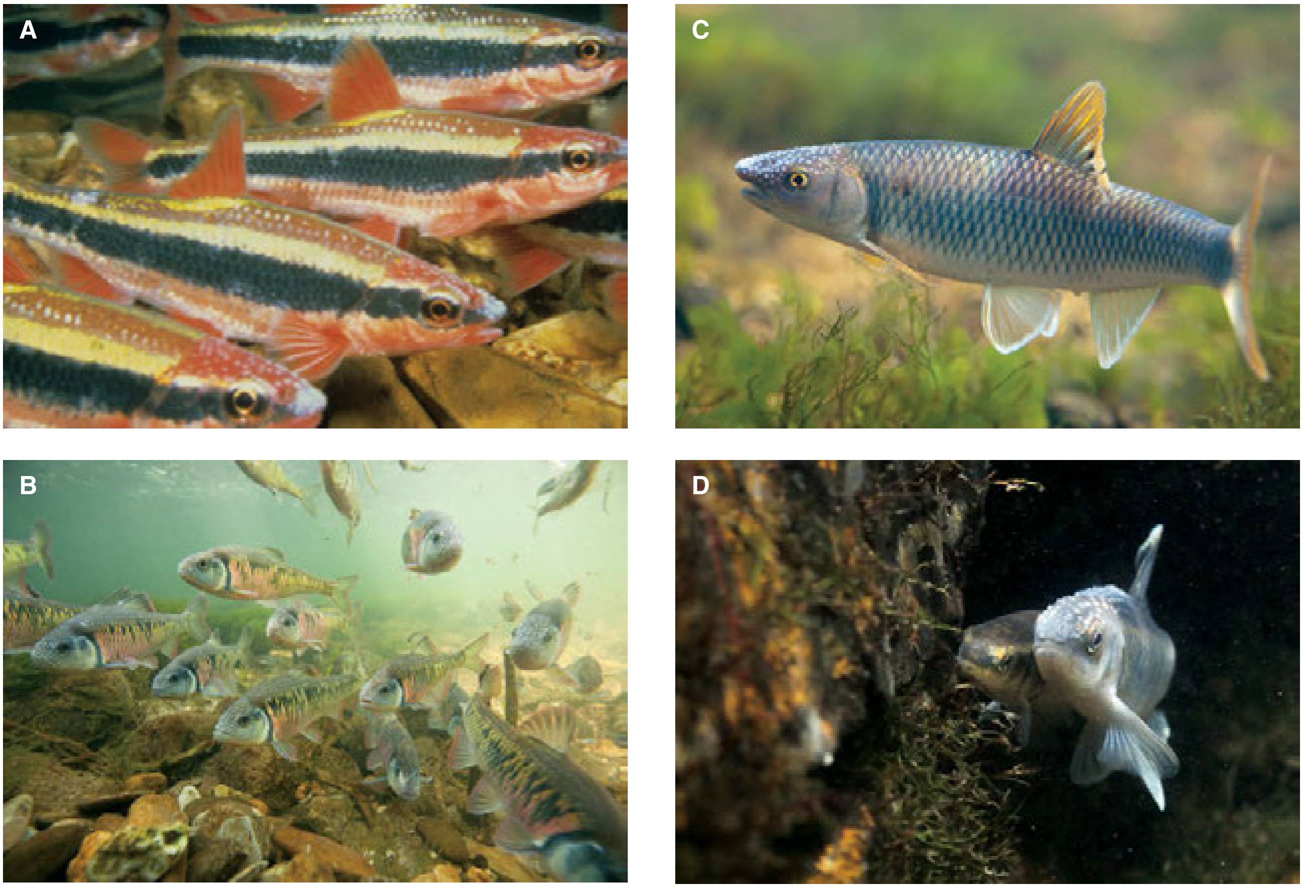


Figure 12.76. (A) A spawning school of tuberculate Cardinal Shiners, *Luxilus cardinalis*, in the Missouri Ozarks in late spring (photograph by and used with permission of W. N. Roston). (B) Brilliantly colored, tuberculate male Striped Shiners, *Luxilus chrysocephalus*, shoaling over the nest of a male River Chub, *Nocomis micropogon*, in the Little River, Blount County, Tennessee (photograph by and used with permission of Dave Herasimtschuk, Freshwaters Illustrated). (C) A tuberculate male Whitetail Shiner, *Cyprinella galactura*, in spawning colors in the Hiwassee River, Polk County, Tennessee (photograph by and used with permission of Jeffrey Basinger, Freshwaters Illustrated). (D) A breeding male Alabama Shiner, *Cyprinella callistia* (*right*), makes a spawning pass along a rock crevice with a female (*left*) (note tubercles on head and dorsum of male) (Conasauga River drainage, Polk County, Tennessee, 29 March 2012; photograph by and used with permission of Lance Merry).

breeding season, most involving changes in color and hypertrophy of the head or other structures (Figs. 12.76 and 12.78; Figs. 12.79–12.82). In the breeding season, several species of *Nocomis* develop a large swelling on the dorsum of the head, often termed a cephalic crest (Fig. 12.78b). The function of these crests is unclear, but they likely act as a visual signal to other males or potential mates, but this has not been tested. Male *Nocomis* also use the tubercle-studded crest to defend the nest against potential egg predators and during territorial battles with conspecific males (Jenkins & Burkhead 1994). Enlarged fins are present in some nuptial male cyprinids, notably the genera *Cyprinella* and *Pteronotropis*. Male *Cyprinella* are territorial crevice spawners (see reproduction section) and develop enlarged dorsal and anal fins when spawning (Fig. 12.76c). The dorsal fin is often strikingly pigmented, and the enlarged fins are likely important for signaling conspecifics. The closely related Bluehead Shiner, *Pteronotropis hubbsi*, and Bluenose Shiner, *P. welaka* (Simons et al. 2000), exhibit the extreme of nuptial fin enlargement; breeding males develop dramatically enlarged and brightly colored dorsal, anal, and pelvic fins (Fletcher & Burr 1992; Boschung & Mayden 2004; Fig. 12.56f).

The genera *Erimonax*, *Erimystax*, *Platygobio*, and *Macrhybopsis* have nuptial pads on the opercle and preopercle

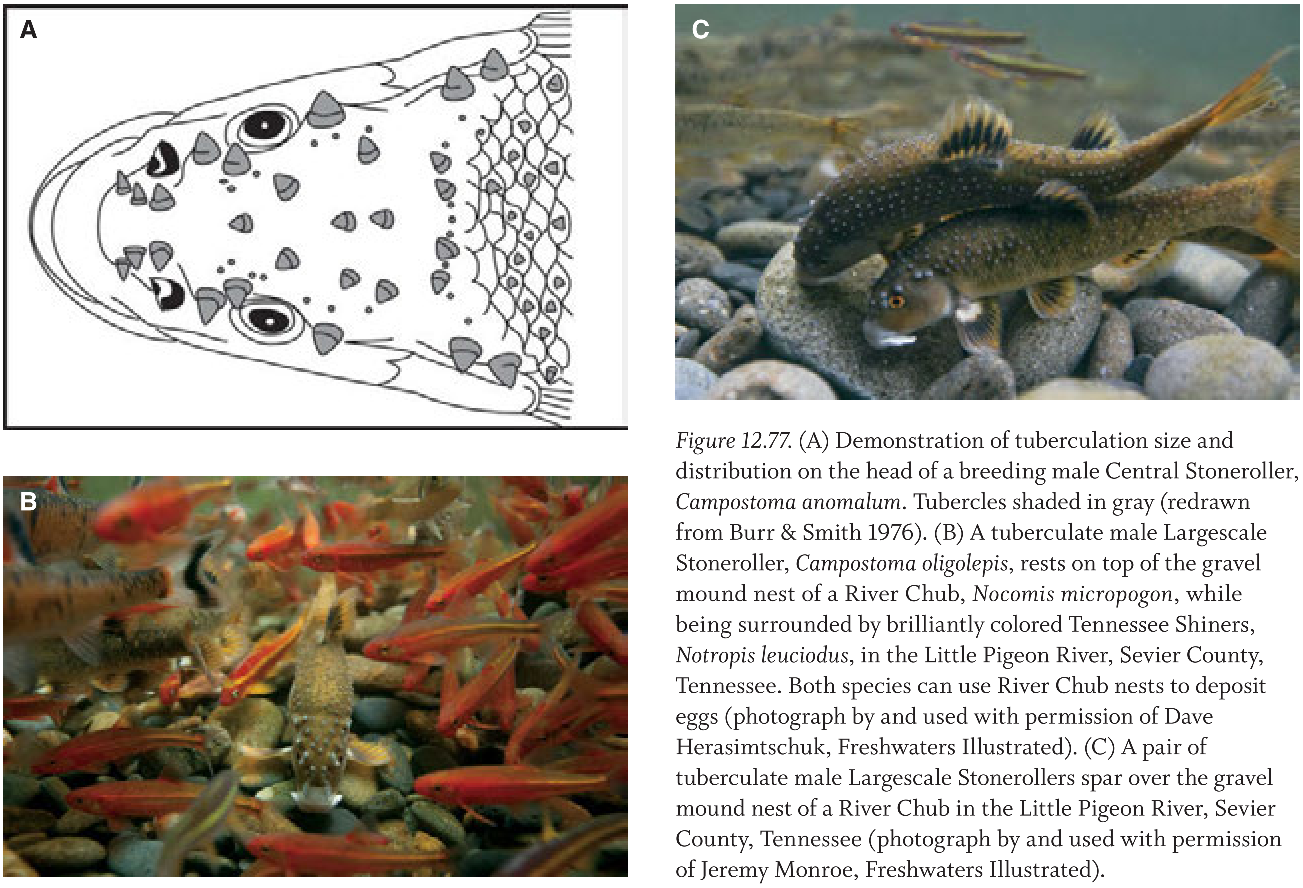


Figure 12.77. (A) Demonstration of tuberculation size and distribution on the head of a breeding male Central Stoneroller, *Campostoma anomalum*. Tubercles shaded in gray (redrawn from Burr & Smith 1976). (B) A tuberculate male Largescale Stoneroller, *Campostoma oligolepis*, rests on top of the gravel mound nest of a River Chub, *Nocomis micropogon*, while being surrounded by brilliantly colored Tennessee Shiners, *Notropis leuciodus*, in the Little Pigeon River, Sevier County, Tennessee. Both species can use River Chub nests to deposit eggs (photograph by and used with permission of Dave Herasimtschuk, Freshwaters Illustrated). (C) A pair of tuberculate male Largescale Stonerollers spar over the gravel mound nest of a River Chub in the Little Pigeon River, Sevier County, Tennessee (photograph by and used with permission of Jeremy Monroe, Freshwaters Illustrated).

(Jenkins & Burkhead 1994; Mayden 1989). These pads may maintain contact during the spawning embrace. The presence of the pads was used to support the monophyly of these taxa (Mayden 1989), although subsequent work on the relationships of these fishes suggested pads arose independently in *Erimystax* and the common ancestor of *Platygobio* plus *Macrhybopsis* (Simons et al. 2003).

Male *Pimephales* develop enlarged pads on the dorsal surface of the head and body that are highly enriched with mucosal cells and are used to deposit mucus on the spawning surface as well as the eggs. Species of *Pimephales* deposit eggs on the ceiling of cavities; the eggs are subsequently guarded by males (Page & Ceas 1989). The mucus may serve three (non-mutually exclusive) purposes: it may aid in egg adherence to the substrate, ease cleaning in terms of debris and damage to the skin of the male, and may serve as a chemical warning to other males (Smith & Murphy 1974). The pad may also be involved in cleansing the eggs and preventing fungal growth (e.g., Jenkins & Burkhead 1994; Ross 2001), although to our knowledge antibiotic properties of the dorsal pad mucus have yet to be demonstrated.

Morphology in Taxonomy and Ecomorphology

External morphology is used widely in studies of systematics, taxonomy, and ecology of fishes (e.g., Hubbs & Lagler 1947; Humphries et al. 1981; Strauss & Bookstein 1982). In North American cyprinids, multivariate morphological analyses have assessed impacts of hybridization on imperiled taxa, distinguished similar endangered species, tested for intra- and interspecific distinctiveness, and correlated morphological and ecological traits.

Conservation of cyprinids has benefited from multivariate morphological studies. Miller & Behnke (1985) used multivariate morphological techniques to assess the impact of hybridization on the endangered Least Chub, *Iotichthys phlegethontis*, with the Utah Chub, *Gila atraria*, and Speckled Dace, *Rhinichthys osculus*. They identified putative hybrids of the Least Chub with the other taxa but did not find strong evidence that hybridization posed a threat to the existence of the species. Similarly, a number of multivariate techniques were used to distinguish morphologically conservative, closely related species of *Gila*, many of which are endangered, in the Colorado River system. This work included a study of the use of qualitative assessment of mor-

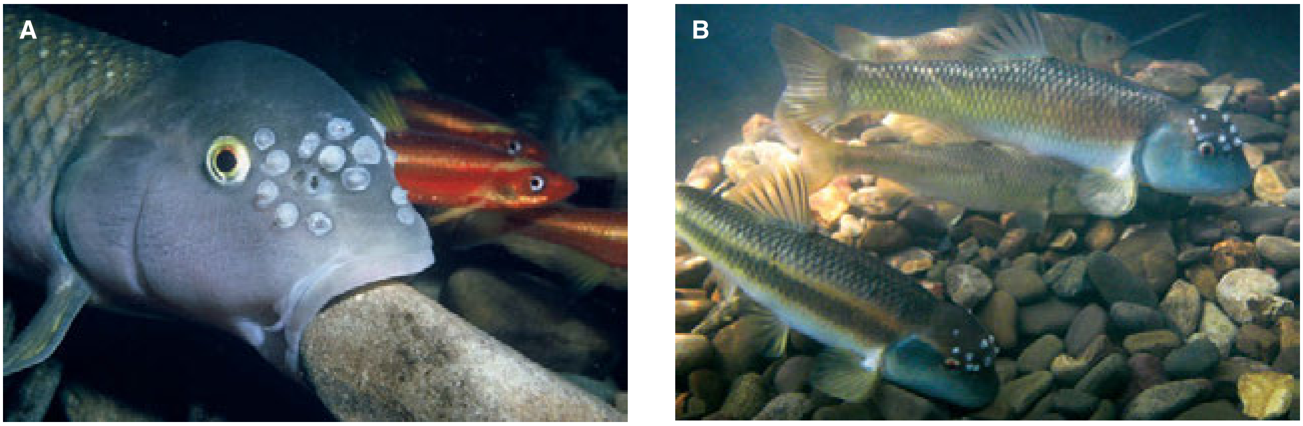


Figure 12.78. (A) A breeding, tuberculate male Bluehead Chub, *Nocomis leptocephalus*, picking up a rock to place on his underwater mound nest. Note the Yellowfin Shiners, *Alburnops lutipinnis*, in the background. Photographed in a stream in Georgia (photograph by and used with permission of W. N. Roston). (B) Two male Bluehead Chubs with swollen heads (cephalic crests) and tubercles typical of breeding season males sit atop a gravel mound nest in Cow Pasture River, Bath County, Virginia (photograph by and used with permission of Jeremy Monroe, Freshwaters Illustrated).

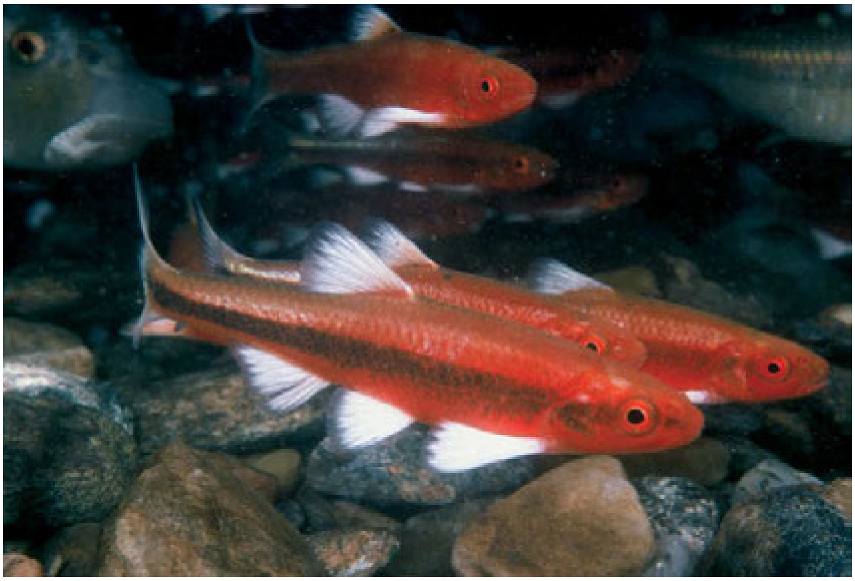


Figure 12.79. The Greenhead Shiner, *Alburnops chlorocephalus*, at its peak breeding color in a stream in the Carolinas (photograph by and used with permission of W. N. Roston).

phology for identification of these rare species (Douglas et al. 1989). Work with rare and endangered species requires quick and accurate identifications made without undue harm to the individual fish. McElroy & Douglas (1995) used videoimaging systems to capture images of the Roundtail Chub, *Gila robusta*, and Humpback Chub, *G. cypha*, for later analyses. Using relative warp analysis (Zelditch et al. 2000), Douglas et al. (2001) could differentiate Roundtail Chubs from Humpback Chubs and could distinguish among populations of the Humpback Chub.

Other studies of cyprinids have used analyses of meristic counts or morphological measurements (or both), as well as pigmentation and tuberculation patterns. These morphological studies evaluated intraspecific distinctiveness, distinguished cryptic cyprinid species, and estimated species relationships (e.g., Schaefer & Cavender 1986; Matthews 1987; Mayden 1988; Carney & Page 1990; Mayden et al. 1991; Humphries & Cashner 1994; Warren et al. 1994; Eisenhour 1999). Morphological characters have also been widely used to help in defining higher-level phylogenetic relationships in Cyprinidae (see phylogenetic relationships section).

Attempts to correlate external morphology with environmental factors and body shape have had mixed success. Felley (1984) used principal components analysis (PCA) to identify morphological and environmental relationships in North American cyprinids using characters that previous investigators hypothesized to be correlated with environment. Even so, habitat use was not predicted with morphological characters taken from functional studies of other fish taxa, suggesting that ecomorphological associations cannot be generalized across fish taxa. A PCA to predict burst swimming performance of 15 North American cyprinds yielded 4 PCA axes as predictors of swimming performance. Nevertheless, after controlling for phylogenetic relationships, morphology no longer predicted swimming performance (Billman & Pyron 2005).

Species that inhabit large streams subject to severe flooding, in particular the large cyprinids of the Colorado River, have a distinctive morphology. Before impoundment, this system was subject to regular, severe flooding with high water velocities. Some cyprinids in this system, particularly the Humpback Chub, *Gila cypha*, have deeply compressed crania with keeled or humped napes (e.g., Bonytail Chub, *G. elegans*; Fig. 12.56e); the fins are large, and the caudal peduncles narrow with high aspect ratio caudal fins; and the scales are reduced or embedded. These traits were presumed to aid swimming in high-velocity environments (Minckley & Meffee 1987; Moyle 2002); however, adults of these species inhabit low-velocity backwaters and experiments using casts of specimens in flow tanks indicated that the keeled or humped napes increase rather than decrease drag (Portz & Tyus 2004). Rather than increasing swimming ability in high velocities, the nuchal humps may increase the effective size of these fishes, allowing them to escape predation by the large, piscivorous Colorado Pikeminnow, *Ptychocheilus lucius* (Portz & Tyus 2004).

On a macroecological scale, typical trends show body size of cyprinids is positively correlated with range size (Taylor & Gotelli 1994) and flow regime (Matthews 1987). In addition, morphologically similar cyprinid species are less likely to co-occur with each other than would be expected by chance (Winston 1995), and fish with more extreme or "far-from-average" morphologies tend to be the most widely distributed (Matthews 1982). These points show that minnows support the widespread notion that morphologically similar fish species pose potential competitive challenges to one another.

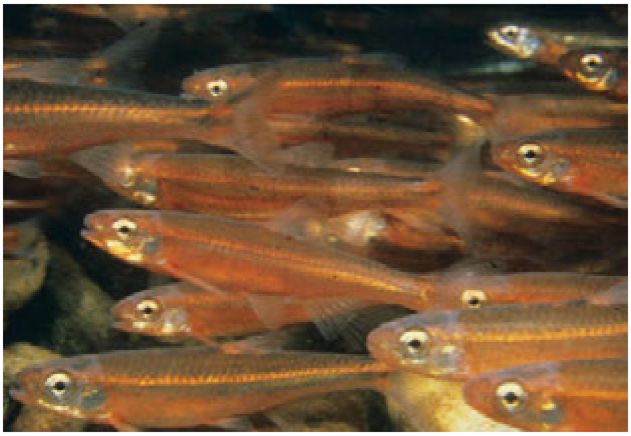


Figure 12.80. The Tennessee Shiner, *Notropis leuciodus*, sometimes forms large schools during the spawning season that number in the thousands (photograph by and used with permission of W. N. Roston).

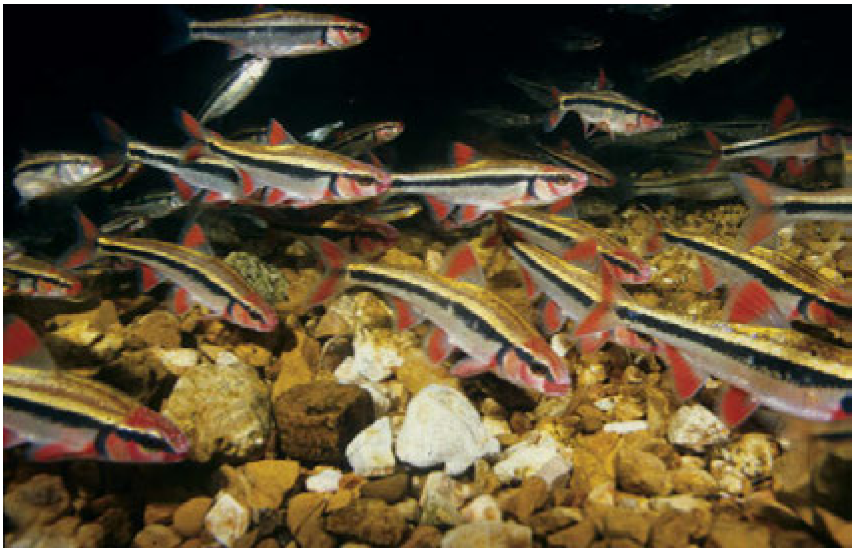


Figure 12.81. A spawning group of Bleeding Shiners, *Luxilus zonatus*, in a stream in the Missouri Ozarks (photograph by and used with permission of W. N. Roston).

GENETICS

A wealth of research is available on genetics of North American cyprinid fishes. Genetic research includes studies of hybridization and introgression; mitochondrial and nuclear genomic evolution; genetic variation in populations; and phylogeography. Cyprinids hybridize extensively where the ranges of closely related species overlap, and hybridization between taxa may be influenced by environmental perturbations. Studies of hybridization in North American cyprinids have provided valuable information on gene flow and introgression in hybrid zones. Hybridization has produced complex clonal lineages and perhaps new species. Work on genomic evolution has identified patterns in the evolution of genome size and of nucleotide variation in the mitochondrial genome. Characterization of genetic variation guides conservation efforts and can be used to infer historical demographic changes in populations. The development of phylogeography has provided valuable information on historical ranges and population structure, information critical to understand biogeographic histories and for conservation and management. North American cyprinid fishes will continue to provide interesting questions for geneticists. More is known about phylogenetic relationships of North American cyprinids than about any other cyprinid fauna. These data coupled with the information provided by the sequencing of the genome of the Zebrafish, *Danio rerio*, a cyprinid native to fresh waters in India, create fascinating opportunities to advance our understanding of genetics of native cyprinids. In this section, the focus is on chromosomes, genome size, hybridization, genetic variation, mitochondrial genomics, and phylogeography.

Chromosomes

Little is known of karyotype evolution of North American cyprinids. This is largely due to the difficulty of examining chromosome variation in these fishes. The chromosomes are small, and gross karyotypic change appears to to be rare (Amemiya et al. 1992). Heteromorphic sex chromosomes have not been observed. The vast majority of species examined have a diploid chromosome number (2n) of 50 and chromosome arm numbers vary between 92 and 100 (Amemiya & Gold 1988). Most work has focused on variation of chromosomes containing the nucleolar organizing regions (NORs). Chromosomal NORs are the sites of the 18S and 28S ribosomal RNA genes. North American cyprinids typically have a single NOR chromosome but may have ≤3 (Gold & Amemiya 1986). In addition to number of chromosomes, variation occurs in the position of the NOR on the chromosome, the centromere position of the chromosome, and the relative size of the chromosome (Gold et al. 1988). Variation in these characters is substantial and species-specific differences are common (Amemiya & Gold 1988; Gold et al. 1988; Gold & Zoch 1990; reviewed by Amemiya et al. 1992).

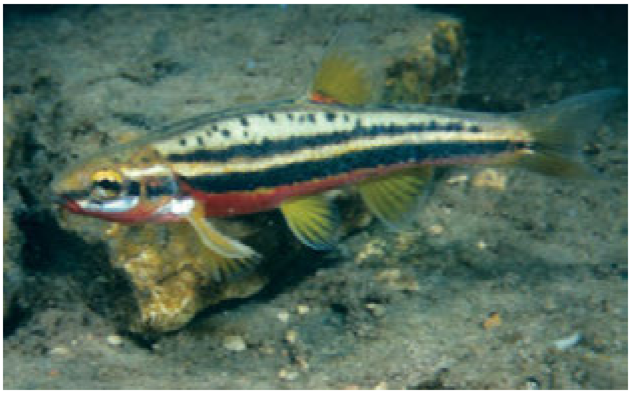


Figure 12.82. A solitary male Southern Redbelly Dace, *Chrosomus erythrogaster*, showing its spawning colors (photograph by and used with permission of W. N. Roston).

Genome Size and Base Substitution

The nuclear genome of North American cyprinids exhibits variation in size among species (Gold & Price 1985). Genome size changes are small, appear to be frequent, and involve both gains and losses of DNA (Gold & Amemiya 1987). Genome size differentiation may occur during speciation episodes (Gold & Amemiya 1987) because the degree of genome size divergence among species of *Notropis* is greater than that among species in other less species-rich genera (Gold et al. 1990). This may be an artifact of classification because phylogenetic work indicates that *Notropis* is polyphyletic (Simons et al. 2003; Mayden et al. 2006; see phylogenetic relationships section).

Hybridization

Hybridization is common among North American cyprinid species (Scribner et al. 2000). Most hybrids occur sporadically, the result of chance events or competition for appropriate spawning substrate. Other combinations may occur regularly, particularly when taxa commonly spawn together; hybrids often occur between nest-building minnows and nest associates (Jenkins & Burkhead 1994). Hybridization also occurs where the ranges of closely related species overlap. The frequency of hybridization may be increased by anthropogenic or other disturbances to the environment and result in hybrid swarms. Hybridization generally has little long-term effects on the parental species because the hybrids are often infertile. Gene flow, however, may occur across hybrid zones, and human-mediated introductions have resulted in local extinction of populations due to hybridization and introgression. Hybridization also may result in the production of clonal species and may even result in the formation of new sexually reproducing taxa. In a review of examples of hybridization in North American fishes, Hubbs (1955) reported more examples of hybridization in cyprinids than any other family. Hybridization usually occurs between closely related species (Gilbert 1961), but intergeneric hybrids are common (Cross & Minckley 1960), some of which were described mistakenly as new species (Hubbs 1951; Hubbs & Bailey 1952; Gilbert 1978).

Hybrids may occur due to changes in water quality, stream flow, or availability of spawning habitat. Some of the most common cyprinid hybrid combinations are the Common Shiner, *Luxilus cornutus*, × Rosyface Shiner, *Notropis rubellus*, and Striped Shiner, *L. chrysocephalus*, × Rosyface Shiner (Gilbert 1961). These species spawn at similar times in similar habitats. Hybridization occurs between the Emerald Shiner, *N. atherinoides*, and Mimic Shiner, *N. volucellus* (Mayhew 1983); both are broadcast spawners in open water. Hybridization is more common where stream flow is greater than preferred by these species (Trautman 1981). Hybrids also may result when species use and compete for the same spawning habitats such as rock crevices (Burkhead & Bauer 1983; Jenkins & Burkhead 1994) or the gravel nests of *Nocomis* and other nest-building taxa (Ross & Cavender 1977; Etnier & Starnes 1993; Jenkins & Burkhead 1994). A high frequency of hybrids occurred in Clark Creek, Mississippi, over a 2-year study (Grady & Cashner 1988) including 4 intergeneric cyprinid crosses: Central Stoneroller, *Campostoma anomalum*, × Southern Redbelly Dace, *Chrosomus erythrogaster*; Central Stoneroller × Bluehead Chub, *Nocomis leptocephalus*; Creek Chub, *Semotilus atromaculatus*, × Southern Redbelly Dace; and Striped Shiner, *Luxilus chrysocephalus*, × Central Stoneroller (Grady & Cashner 1988). Three of these (*Nocomis*, *Campostoma*, and *Semotilus*) construct gravel nests for spawning, and species of *Chrosomus* and *Luxilus* are common nest associates of these taxa (Johnston & Page 1992). Spawning habitat in Clark Creek is limited, and areas with gravel substrate are restricted. Thus, nest crowding may result that could increase the frequency of hybridization. Electrophoretic analysis of parental species from this stream did not reveal introgression (Grady & Cashner 1988), suggesting infertility of or selection against F_1 hybrids.

Human activities can increase frequency of hybridization, producing hybrid swarms. In the Guadalupe River, Texas, the Red Shiner, *Cyprinella lutrensis*, and Blacktail Shiner, *C. venusta*, co-occur. In clear, undisturbed streams, little if any hybridization occurs between these species. Hybridization and introgression of Red Shiners and Blacktail Shiners were associated with increased turbidity and pollution from human activities (Hubbs & Strawn 1956). In the Guadalupe River, large numbers of hybrids occurred where gravel-mining operations in the river greatly increased turbidity.

Introduction of non-native cyprinids can result in hybridization with native cyprinids. The Arroyo Chub, *Gila orcutti*, was introduced into the Mohave River system, California, where it hybridized with the native Mohave Tui Chub, *Siphateles bicolor mohavensis* (Hubbs & Miller 1943). Hybrids increased in numbers relative to the parental forms, and the native parental species were completely replaced (Hubbs 1955; Moyle 2002). The Mohave Tui Chub now persists in a single isolated pond (Moyle 2002). The case of the Mohave Tui Chub has grave implications for conservation of rare cyprinids given the ease with which they hybridize and the increasing number of instances of species transported beyond their native range (Fuller et al. 1999).

Hybridization may occur regularly where the ranges of closely related taxa overlap. The best-studied example of hybridization in North American cyprinids is between the closely related Common Shiner, *Luxilus cornutus*, and Striped Shiner, *L. chrysocephalus*. The Striped Shiner is distributed widely in eastern North America, ranging from Oklahoma to western New York and Pennsylvania and from Gulf Coast drainages, Mississippi and Alabama, north to Michigan and southern Ontario (Gilbert 1961; Page & Burr 2011). The Common Shiner has a more northerly distribution, occurring from Nebraska and Colorado east to Massachussets and New Brunswick and from Missouri north to southern Ontario (Gilbert 1961; Page & Burr 2011). These species are sympatric in an area that extends from southeastern Wisconsin and northeastern Illinois, east to western Pennsylvania and New York (Gilbert 1961). Within this zone of sympatry, the distribution and abundance of hybrids varies substantially. In some rivers, hybrid individuals are common, but in other rivers, hybrids are rare or completely absent (Gilbert 1961). Even where hybrids are common, electrophoretic studies revealed consistent heterozygote deficiencies, indicating that species identity was maintained across the zone of sympatry (Dowling & Moore 1984; see also Gleason & Berra 1993). The maintenance of species identity and lack of extensive introgression is maintained partly by selection against adult hybrids with the frequency of hybrids present in a cohort decreasing at a rate of 9.2%/year (Dowling & Moore 1985a). Morphological, electrophoretic, and mitochondrial DNA data indicated that F_1 hybrids were relatively rare, and most hybrid individuals were the result of several generations of backcrossing. Hybrids were often common and could outnumber one of the parental species. In areas of sympatry, population sizes of the parental species were unequal; the rare species had a higher proportion of introgressed alleles than the common species. Thus introgression was largely unidirectional (Dowling et al. 1989), but the direction of introgression varied depending on location. In F_1 hybrids and backcrosses from populations in the Illinois River drainage and tributaries to Lake Michigan, mtDNA haplotypes of the Common Shiner were more common than Striped Shiner haplotypes. In populations from the Wabash River and tributaries to Lake Erie, the direction of backcrossing was generally in the reverse direction although a considerable amount of variation occurred between populations (Dowling et al. 1997). During the Pleistocene, Lake Michigan and Lake Erie were not connected, and each drained southward by separate rivers (Bailey & Smith 1981). Thus, the variation in the direction of introgression in hybridizing populations of *Luxilus* may be a function of historical and frequency dependent effects (Dowling et al. 1997). Further, the hybrid zone appears to have shifted northward. The frequency of Common Shiner haplotypes in samples of Striped Shiners increases away from the area of sympatry (Dowling & Hoeh 1991).

Clonal Lineages and Hybrid Species

Hybridization between closely related vertebrates may result in clonal lineages. These may be parthenogenetic, hybridogenetic, or gynogenetic lineages. Examples include lizards, frogs, salamanders, and fishes (Schultz 1969; Vrijenhoek et al. 1978 and references therein). In North America, the Northern Redbelly Dace, *Chrosomus eos*, and Finescale Dace, *C. neogaeus*, are widespread across the northern United States and Canada east of the western Continental Divide and may hybridize where they co-occur. Hybrids between these species are common where they occur and are often more numerous than the parental species (Dawley et al. 1987). The vast majority of the hybrids are females and may even be present in the absence of one of the parental species, suggesting clonal reproduction (Hubbs 1955; New 1962). Investigations into the genetics and mode of reproduction of these hybrids indicate a complex system different from that of clonal poeciliids.

In the *Chrosomus eos-neogaeus* system, hybrids are present as diploids, triploids, or mosaics; mosaics contain both diploid and triploid cells (Dawley et al. 1987; Dawley & Goddart 1988). Diploids are hybrids between the parental species and contain a single copy each of the *C. eos* and *C. neogaeus* genomes (Dawley et al. 1987). Diploid hybrid females are gynogenetic clones, producing diploid ova that require sperm from one of the parental species to initiate cell division (Goddard & Dawley 1990). Graft transfer experiments demonstrated that diploid offspring of the hybrid females are genetically identical to their mother (Dawley et al. 1987). All diploid clones in a population are genetically identical (Elder & Schlosser 1995), but clones between populations may not be genetically identical, indicating multiple origins for clones (Goddard et al. 1989). Triploid hybrids contain the *C. eos-neogaeus* genome plus the haploid genome from either *C. eos* or *C. neogaeus* (Dawley et al. 1987). Triploid offspring result from fertilization of the eggs of hybrid clonal females with one of the parental species (Goddard & Dawley 1990). Fin graft implants from diploid clones into triploids are not rejected, indicating that the triploids are inheriting the entire clonal maternal genome of *C. eos-neogaeus* (Dawley et al. 1987). Triploids are the result of egg activation and fertilization (Goddard & Dawley 1990). Most triploid individuals are females; the few triploid males appear unable to produce viable sperm (Goddard & Dawley 1990). At least some triploid females can reproduce. Oocytes of triploids appear to undergo reductive division, producing haploid ova that contain only the *C. eos* genome (Goddard & Schultz 1993); the paternal and the maternal *C. neogaeus* genomes are discarded. Crossing over may take place during meiosis because some *C. neogaeus* characteristics are evident in crosses of triploids with male *C. eos* (Goddard & Dawley 1990; Goddard & Schultz 1993).

Mosaic individuals contain both diploid and triploid cells (Dawley & Goddard 1988). The diploid cells contain the clonal *C. eos-neogaeus* genome, and the triploid cells contain the clonal *C. eos-neogaeus* genome plus the haploid genome from one of the parental species. Mosaics appear to result from egg activation followed by a delayed fertilization of a cell after cell division of the embryo has commenced. The ratio of diploid to triploid cells in a mosaic individual is variable, and different tissues may exhibit variation in ploidy. This includes the oocytes as evidenced by reproduction of mosaic individuals. Diploid oocytes produce diploid ova that may or may not be fertilized, resulting in clonal, mosaic, or triploid offspring. Triploid oocytes produce haploid ova that must be fertilized (sexual reproduction), resulting in diploid offspring (Goddart & Schultz 1993). The results of these interactions are clonal, diploid lineages of hybrid origin that produce triploid and mosaic offspring in the presence of one or more parental species. The clonal gynogens may facilitate limited introgression between parental species by production of sexually reproducing triploid and mosaic individuals. Thus, the *C. eos-neogaeus* system displays a complex pattern of parental and hybrid species. *Chrosomus eos* and *C. neogaeus* are not sister-taxa (Strange & Mayden 2009), demonstrating that the potential to hybridize may be plesiomorphic in a particular clade and thus an unreliable predictor of relationship.

Hybridization also may result in the formation of new self-perpetuating species that can exist independently from parental taxa. The importance of hybridization to speciation of North American cyprinids is unknown and probably underestimated due to the difficulties of identifying hybrid taxa that are not of recent origin. The Virgin River Chub, *Gila seminuda*, may be of hybrid origin, the result of hybridization between the Roundtail Chub, *G. robusta*, and Bonytail Chub, *G. elegans* (Smith et al. 1979). The Virgin River Chub is known only from the Virgin River, Arizona, Nevada, and Utah, and is not sympatric with Roundtail Chub or Bonytail Chub. DeMarais et al. (1992) examined morphological, allozymic, and mtDNA variation in the Virgin River Chub, Roundtail Chub, and Bonytail Chub as well as morphology of captive-raised F_1 hybrids of the Roundtail Chub and Bonytail Chub. They concluded that the Virgin River Chub is the result of Pleistocene or post-Pleistocene hybridization and suggested that the Roundtail Chub of the Muddy River (formerly Moapa River), Nevada, is also of hybrid origin. Hybridization among species of *Gila* is widespread and well documented. Introgressive hybridization may play a major role in the evolution of diversity of this group, allowing adaptation to dramatic changes in the environment since the Pliocene (Dowling & Demarais 1993; Gerber et al. 2001).

A controversial example of putative hybridization is the case of the Cheat Minnow, *Rhinichthys bowersi*. Goldsborough & Clark (1908) described this species; Raney (1940) redescribed this fish as a hybrid River Chub, *Nocomis micropogon*, × Longnose Dace, *Rhinichthys cataractae*. Since then the Cheat Minnow has been considered a hybrid, but its status as a self-perpetuating species of hybrid origin or as an occasionally produced F_1 hybrid is in debate. In a description of the morphology and distribution of all known hybrid individuals, Stauffer et al. (1979) found that the Cheat Minnow occurred throughout the upper Cheat River system, West Virginia, with occasional reports from elsewhere in the Monongahela River system, West Virginia and Pennsylvania. Goodfellow et al. (1984) concluded that the biochemical data supported recognition of the Cheat Minnow as a self-perpetuating species of hybrid origin. Individual Cheat Minnows exhibited unique enzyme mobilities at several loci, and mixtures of tissue extracts from preserved parentals were not identical as would be expected if these were F_1 hybrids. Stauffer et al. (1997) described morphological variation and several unique features not found in the presumed parental species and argued that intermediacy in morphology was not prima facie evidence that these fish were F_1 hybrids. They pointed to the results of Goodfellow et al. (1984); the persistence of Cheat Minnows in the Monongahela River system over the last 100 years; the large number of specimens collected in 1986; and unique morphological characters to justify recognition of the Cheat Minnow as a self-perpetuating species of hybrid origin. They then erected a new genus, *Pararhinichthys*, to contain this species, a classification considered necessary given the presumed hybrid origin of the taxon.

In contrast, Poly & Sabaj (1998) stated that previous work was insufficient to determine whether the Cheat Minnow is an F_1 hybrid or a self-perpetuating species. They criticized the techniques of Goodfellow et al. (1984), arguing that simple mixing of tissue extracts is insufficient to allow formation of hybrid enzymes that might display the mobilities observed in the putative hybrids. They also criticized the interpretation of other data presented in that paper and argued that the morphological evidence of Stauffer et al. (1997) could be interpreted a variety of ways. Interestingly, Poly & Sabaj (1998) concluded that the Cheat Minnow is best considered an F_1 hybrid even though they presented no new evidence to support either possibility. Review of the published data suggests that all the evidence collected to date is equivocal. Indeed, the Cheat Minnow may not even be of hybrid origin. A well-designed test requires examination of molecular data from a variety of loci in several individuals, a tall order given the rarity of this fish.

Genetic Variation

Knowledge of genetic variation in cyprinids is based on studies to determine taxonomic status, to inform and measure success of conservation efforts, to examine effects of rapid range expansion, and to assess impact of presumed hazardous wastes on populations. Most assessment of genetic variation in North American cyprinids assayed allozymes using starch gel (non-denaturing) electrophoresis to describe variation within and between populations of a species (Merritt et al. 1978; White 1987). More recent studies are incorporating molecular techniques such as DNA sequencing or microsatellite variation.

The earliest studies of genetic variation in North American cyprinids examined variation within and among the California minnows, the Hitch, *Lavinia exilicauda*, and California Roach, *Hesperoleucas symmetricus* (Avise et al. 1975; Avise & Ayala 1976). The two species were similar biochemically, a similarity more typical of interpopulational variation than interspecific variation, leading to a proposal to place both taxa in the genus *Lavinia*.

The vast majority of work on genetic variation in North American cyprinids has focused on the conservation biology of southwestern taxa (e.g., Rosenfeld & Wilkinson 1989; Demarais et al. 1993). Many southwestern fishes are imperiled, primarily due to habitat destruction. Species have been fragmented with some populations reduced to small numbers of individuals, and in some cases natural recruitment is low or nonexistent. Management plans for rare and endangered species should include strategies for maintaining as much genetic variation as possible (Meffe 1986; Meffe & Vrijenhoek 1988; Ryman 1991), sometimes a challenge when populations are reduced to a few individuals. The Bonytail Chub, *Gila elegans*, is a large cyprinid (Fig. 12.56e) native to the Colorado River system. This species requires flowing water and gravel bars for spawning and survival of juveniles. The adults can live in reservoirs, but little or no successful spawning or recruitment has occurred since the 1950s (Minckley et al. 1989). In 1981, 10 adult, wild-caught fish, 30–50 years in age, were spawned artificially at the U.S. Fish and Wildlife Service Dexter Fish Hatchery, New Mexico (Hamman 1982). Mean heterozygosity for F_2 progeny was 0.026 ± 0.017. This is somewhat, but not substantially, lower than the mean heterozygosity estimated in a survey of North American cyprinids (Avise 1977). Minckley et al. (1989) attributed this relatively high amount of genetic variation to the technique used for spawning the wild-caught individuals. Hamman (1982) carefully mixed the eggs of each female with the milt from a separate male, thus maintaining as much genetic variation as possible in the captive population.

The Colorado Pikeminnow, *Ptychocheilus lucius*, is another large cyprinid severely impacted by impoundments on the Colorado River. Heterozygosity in this species is relatively high, 2.6–5.3%, especially considering the recent decrease in population size (Ammerman & Morizot 1989). Little evidence exists of variation between populations in the Green and Colorado Rivers. This suggests that *P. lucius* may have exhibited population-level variation in the past, but this variation was largely obscured by stocking efforts and habitat alterations (Morizot et al. 2002).

Coalescent theory, using DNA sequence data to estimate long-term female effective population size, provides historical information on long-term fluctuations in abundance. The Humpback Chub, *Gila cypha*, exhibits a pattern of genetic variation consistent with that expected for a constant-sized population at equilibrium (Garrigan et al. 2002). Although the numbers of Humpback Chubs have declined substantially since impoundment of the Colorado River system, declines were localized, and thus genetic variation was maintained across the system in spite of the recent bottleneck. This contrasts starkly with the Bonytail Chub, which exhibits extremely reduced variation in mitochondrial DNA sequences. This is not surprising since captive stock was subjected to an extreme bottleneck; the extant population is descended from 10 individuals (Hamman 1982, see second paragraph above). Genetic evidence for bottlenecks also was demonstrated in the endangered Virgin River Chub, *Gila seminuda*, following a misapplication of rotenone to control invasive fish species (Demarais et al. 1993).

Rapid range expansion or leading edge expansion, as observed in colonization of previously glaciated areas, results in reduced genetic variation (Hewitt 1996) and this reduction may be substantial enough to overcome effects of natural selection at most loci (Girard & Angers 2011).

Longnose Dace, *Rhinichthys cataractae*, are widespread in glaciated areas of the northern United States and much of Canada east of the Continental Divide, an area formerly covered by the Laurentian ice sheet. Populations in glaciated areas have markedly reduced allelic diversity on both coding and non-coding loci, suggesting that neutral demographic processes have shaped genetic diversity (Girard & Angers 2011). This study included a locus that is part of the major histocompatibility complex (MHC) that is responsible for immune responses to viral and bacterial infections. This observation was surprising as variation in MHC loci is considered essential for long-term health of populations (Bernatchez & Landry 2003). In a comparison of two subsets of Longnose dace populations, Girard & Angers (2011) found no evidence of short-term selective effects in 10 populations, but in 9 populations they identified increased allelic diversity at an MHC locus that departed from expectations of neutrality. This observation is consistent with balancing selection on this locus, suggesting that these populations at least are subject to recent selection on the MHC.

Anthropogenic structures, such as dams, can influence genetic variation between populations. Hydroelectric dams can release cold water from the hypolimnion of the reservoir, and lower temperatures can persist for a significant distance downstream. In the Brazos River, Texas, discharge from the Morris Sheppard Dam during power generation results in an average temperature drop of 4°C, 1 km downstream. Red Shiners, *Cyprinella lutrensis*, from populations downstream of the dam have distinctly different temperature preferences from those above the dam, 30.0°C and 23.3°C, respectively (Calhoun et al. 1982). The temperature preferences are accompanied by concordant allozyme variation and thermal tolerance, as measured by the thermal critical maximum (TCM; measured at the upper temperature of loss of equilibrium) (King et al. 1985; see physiology section). A significant correlation exists between the distance from the dam and the mean TCM and is accompanied by a decrease in genetic heterozygosity with distance from the dam. The higher heterozygosity may be adaptive given the variability of the thermal habitat immediately below the dam. Populations above and below the dam had been separated for 42 years at the time of the study, and the genetic and physiological differences reflect the strong selection and rapid adaptation to the thermal variability of the downstream habitat (King et al. 1985).

Skalski et al. (2008) used microsatellite loci to examine genetic diversity among populations of the Creek Chub, *Semotilus atromaculatus*, in tributaries of the Eno River, South Carolina. Upstream tributaries flowed into riverine habitat, and downstream tributaries flowed into the Falls Lake Reservoir. Populations in riverine tributaries had higher genetic diversity than populations in reservoir tributaries. These data suggest that reservoir tributaries exhibit decreased effective population size relative to riverine tributaries. Although these results are correlative and these differences may have existed prior to impoundment, it is likely that impoundment has decreased migration between populations, leading to the observed decrease in genetic diversity.

Mitochondrial Genome

North American cyprinids have been used to examine molecular mechanisms governing variation in the mitochondrial genome. It is generally accepted that mitochondrial genes have different substitution rates and that some of these rates are a function of selection acting on nonsynonymous substitutions that affect function of the gene product (RNA or proteins). This does not explain base compositional bias or gene-specific variation in synomyous substitutions. Among several species of *Notropis*, adenosine-guanine transitions were saturated but thymine-cytosine transitions were not (Bielawski & Gold 1996). The rate of synonymous substitution of NADH dehydrogenase 4L also was lower than cytochrome *b*. Evidence exists for strand-specific bias and a mutation gradient in three mitochondrial genes. Substitution rates decreased with distance from the origin of H-strand replication. This is likely a result of the mechanism of replication of the mitochondrial genome. During replication, the H-strand is single stranded and thus more vulnerable to damage (mutation) than the L-strand. Because of the direction of replication, genes closer to the origin of H-strand replication experience a higher mutation rate and thus a larger amount of synonymous substitutions (Bielawski & Gold 2002). Broughton & Dowling (1994) examined a tandem duplication of 260 base pairs in the mitochondrial control region of the Spotfin Shiner, *Cyprinella spiloptera*, in which each specimen had two or three copies of this repeat. Similarity of the repeats suggested they were produced by a single mechanism, but the duplications had occurred multiple times. A model associated with light strand synthesis was outlined to explain this complex pattern of mitochondrial diversity. In a following paper (Broughton et al. 1998), a strange pattern of nucleotide variation in Spotfin Shiners was described, in particular an eight base pair deletion and an adjacent adenine to guanine transition (the G/deletion). Phylogenetic analyses revealed that the G/deletion had occurred multiple times, an unexpected result given that insertion and deletion events are considered to be relatively rare. The pattern of variation suggested a non-random deterministic mechanism of mutation, possibly due to replication errors associated with secondary structure on the DNA template. This work raises the specter that convergences due to specific mechanisms of mutation might be more common than currently thought, which may hamper reconstruction of phylogenetic relationships.

Phylogeography

The study of phylogeography has provided substantial information on the geographical variation within and among populations of fishes, including many cyprinids. Fish populations are particularly prone to isolation and subsequent divergence because they are restricted to aquatic habitats. This is not to say that fishes are not capable of large-scale dispersal. Phylogeographic studies of several species have indicated the potential for dispersal and gene flow across large distances; this is perhaps most notable where species dispersed north following the retreat of the ice sheets after the Pleistocene glaciations. Reduced genetic variation in populations is consistent with colonization of previously glaciated areas (see above) and can be used to reconstruct the history of colonization of drainages. Tipton et al. (2011) demonstrated that three drainages, the Housatonic, Connecticut, and Thames Rivers, were colonized by a single population of the Blacknose Dace, *Rhinichthys atratulus*, via Glacial Lake Connecticut (now Long Island Sound). The Housatonic River was subsequently colonized by a second, western source, presumably from the Hudson River drainage. Analysis of diversity of the mitochondrial cytochrome *b* gene within and between populations of the Speckled Dace, *Rhinichthys osculus*, in Oregon revealed deep genetic divergences between populations and suggested that these reflected Miocene or Pliocene vicariant events. In addition, two divergent lineages are present in the Klamath River basin (Pfrender et al. 2004). These divergent mitochondrial lineages possibly are indicative of multiple species within this clade, but additional morphometric or nuclear sequence data are needed to bolster this hypothesis.

Cyprinids from the arid Southwest have similar patterns of deep divergence between populations. The Little Colorado Spinedace, *Lepidomeda vittata*, exhibits low patterns of genetic variation but a high degree of population structure, suggesting that current populations are derived from a single large population whose range was subsequently fragmented (Tibbets et al. 2001). Similar patterns occur in the Spike Dace, *Meda fulgida*, and Loach Minnow, *Tiaroga cobitis* (Tibbets & Dowling 1996). In contrast, the Longfin Dace, *Agosia chrysogaster*, apparently had high levels of gene flow between populations (Tibbets & Dowling 1996). The Longfin Dace has been less affected by anthropogenic disturbances of its habitat than the Spike Dace and Loach Minnow and also has greater dispersal capabilites. Thus, the patterns of genetic variation observed are likely due to both long-term and short-term factors.

Fragmentation of habitats can have lasting impacts on the genetic variation in fish populations. The rapid draining of Lake Bonneville, 14,500 years ago (Jarrett & Malde 1987), followed by dry climatic conditions, resulted in fragmentation of the once large lake (51,700 km^2; Oviatt et al. 1992) into disjunct springs, lakes, and rivers. This dramatically affected the fish fauna. Phylogeographic variation in the Utah Chub, *Gila atraria*, which is native to the Lake Bonneville Basin and the upper Snake River system, showed great divergence between Snake River and Lake Bonneville populations, indicating a Pliocene or Early Pleistocene divergence, predating the draining of Lake Bonneville (Johnson 2002). Nevertheless, within the Lake Bonneville basin, Utah Chub populations are isolated, and the degree of genetic divergence among populations is consistent with the post-Pleistocene draining of the lake and subsequent climatic conditions.

Gulf Coast and Atlantic Slope drainages have a complex history that is reflected in the distribution of their fish fauna. The fauna of this area is reviewed by several authors in Hocutt & Wiley (1986), but most papers in that volume explain fish distributions using only hypotheses of dispersal. Mayden (1985a, 1987, 1988) and Wiley & Mayden (1985) proposed a series of vicariant hypotheses to explain diversity and distribution of fishes of the Mississippi River basin and Mobile Basin, particularly those in the Eastern, Ouachita, and Ozark Highlands. A few phylogeographic tests of these hypotheses are available using cyprinid species.

In phylogeographic studies of the Bigeye Chub, *H. amblops*, the *Notropis rubellus* species group, and the Bluehead Chub, *Nocomis leptocephalus*, each clade provided evidence of Pliocene or later divergence (Berendzen et al. 2008ab; Nagle & Simons 2012). Bigeye Chub populations exhibited signs of population fragmentation in the Ozark and Eastern Highlands that dated to the Pleistocene or before. The *N. rubellus* species group could be divided into seven species, three of which are undescribed. Northern species in this group (Carmine Shiner, *Notropis percobromus*; Rosyface Shiner, *N. rubellus*; *N.* sp., Ohio River; and *N.* sp., New River–Atlantic Slope) exhibited signs of recent northward range expansion into previously glaciated areas. Waterfalls also were implicated as barriers to gene flow. Kanawha Falls formed a barrier between the undescribed Ohio River form and the undescribed New River–Atlantic Slope form. Both lineages are reciprocally monophyletic and exhibit genetic divergence datable to the Pleistocene. Cumberland Falls on the Cumberland River also formed a barrier to gene flow between the Highland Shiner, *Notropis micropteryx*, below the falls and the undescribed Ohio River form, distributed in the Ohio River drainage and in the upper Cumberland River above the falls. These species are not sister-taxa. Nagle & Simons (2012) demonstrated the existence of undescribed diversity within the Bluehead Chub, *Nocomis leptocephalus*, on the Gulf and Atlantic Slopes. They suggested that this diversity was due to rapid speciation early in the Pleistocene. This increase in diversification rate was coincident with prehistoric climate change and was likely driven by fragmentation of ancient drainages.

The Streamline Chub, *Erimystax dissimilis*, exhibits interesting patterns of both widespread gene flow and isolation (Simons 2004). Although populations of the Streamline Chub are isolated and disjunct, the observation of shared haplotypes in populations close to the extremes of the range and similar haplotypes in most populations suggests recent gene flow between populations. Isolation of extant populations thus may be a factor of anthropogenic effects on the environment, including dredging and impoundment of large rivers; isolation is illustrated by the Green River populations, Kentucky. The Green River is located in the center of the range of the Streamline Chub yet contains widely divergent haplotypes consistent with a pre- or Early Pleistocene divergence. The Green River also contains individuals with mitochondrial haplotypes from the widespread clade. This pattern may be due to post-Pleistocene dispersal into the Green River system, range expansion from a Green River refugium where the dispersers were sampled from one of the two Green River clades, or isolation of the Green River with incomplete lineage sorting in this drainage.

Phylogeography also provides evidence of dispersal or range expansion in *Erimystax*. In the Gravel Chub, *Erimystax x-punctatus*, individuals from the Meramec River, Missouri, are similar genetically to individuals from the upper Iowa River, Minnesota and Iowa (Simons 2004). This pattern suggests post-Pleistocene dispersal from an Ozark refugium into the upper Mississippi River. Similar patterns occur in the Carmine Shiner, *Notropis percobromus* (Berendzen 2008a); the genus *Hypentelium* (family Catostomidae) (Berendzen et al. 2003); and the genus *Percina* (family Percidae) (Near et al. 2001). Examination of other taxa likely will show the same pattern.

Given the large number of widely distributed cyprinid taxa in eastern North America, comparative phylogeographic studies of these fishes have the potential to distinguish dispersal events and allow identification of common patterns of deep divergence between populations and higher taxa. This approach may allow recovery of the complex patterns of stream capture and other geological changes in this region.

PHYSIOLOGY

The Fathead Minnow, *Pimephales promelas*, can be considered the "white lab rat" of North American minnows. Much of our current knowledge about cyprinid physiology—and about fish physiology in general—stems from work on this single species. Nearly exclusive study of this single fish species is a double-edged sword. On one hand, we have a highly in-depth understanding of the nuanced interplay between physiological stressors, giving toxicologists the opportunity to study huge numbers of potential toxins and their interactions (Russom et al. 1997). We also have a deep knowledge of chemical communication within this species (see following subsection). Obversely, however, understanding of the diversity of sensitivities and physiological capabilities in different cyprinid taxa is severely limited. What little is known suggests that North American cyprinids are diverse physiologically and have the potential for a wealth of comparative work. We divide our review into four areas: sensory physiology; growth and digestion; environmental tolerance and osmoregulation; and cyprinid toxicology.

Sensory Physiology

One of the most striking and unique aspects of how cyprinids sense their environment is the use of pheromones to communicate with conspecifics. Alarm substance cells (ASCs) are one such pheromone communication mechanism that has been studied intensely in Fathead Minnows.

These are specialized cells in the epidermis that rupture when subjected to relatively minor damage, releasing their contents into the surrounding water. The cells contain an alarm substance that triggers anti-predator behaviors in conspecifics and in some cases, heterospecifics (see behavior section). The alarm pheromone is thought to consist of a purine skeleton with a nitrogen oxide functional group (see Pfeiffer et al. 1985), although a host of nitrogen oxide–containing aromatic compounds may be present in the alarm pheromone system (G. E. Brown et al. 2000, 2001ce). A pyridine-N-oxide also elicits anti-predator behavior, emphasizing the importance of the nitrogen oxide functional group because other similar compounds without nitrogen oxide groups do not elicit a response (G. E. Brown et al. 2000). Alarm pheromones are sensitive to pH and can be irreversibly changed, and thus rendered ineffective, by lowered pH (Brown et al. 2002). This pattern occurred in Fathead Minnows and Finescale Dace, *Chrosomus neogaeus*, as well as with natural (skin extract) and artificial (synthesized) alarm pheromone compounds. Gustatory and single-celled chemosensory systems were not effective at recognizing predator and alarm-substance odors and only the olfactory epithelium contained the receptors for the alarm pheromone (Chivers & Smith 1993; see also behavior section).

The Weberian apparatus (see morphology section) has often been postulated to enhance acoustic sensitivity in cyprinids. Despite this interesting morphological trait, acoustic signaling has not been studied intensely in North American cyprinids. In investigations of auditory sensitivity in Fathead Minnows, auditory thresholds could be increased after exposure to white noise for 24 h, and at some frequencies, thresholds could be increased significantly in as little as 1 h (Scholik & Yan 2001). Recovery of the threshold was dependent on the frequency that the fish was exposed to as well as the duration of that exposure. Threshold shifts lasted >2 weeks (see also reproduction section).

Growth and Digestion

One of the most important aspects of growth in fishes is the seasonal timing of shifts in energy allocation from growth to reproduction. Reproductive strategies of many cyprinids indicate a bet-hedging strategy, whereby multiple clutches are produced by a female during a single spawning season, presumably to account for local, short-lived periods when the environment is not conducive to fast growth and high recruitment. Durham & Wilde (2005) investigated the effects of such a bet-hedging strategy on first-summer growth of five minnow species: Arkansas River Shiner, *Notropis girardi*; Peppered Chub, *Macrhybopsis tetranema*; Plains Minnow, *Hybognathus placitus*; Flathead Chub, *Platygobio gracilis*; and Red Shiner, *Cyprinella lutrensis*. In these taxa, individuals hatched earlier in the summer generally exhibited higher growth rates. They proposed two hypotheses explaining these results. First, temperatures near or exceeding thermal optima for growth later in the breeding season could result in a decreased rate of growth. Second, size of the spawning fish may result in greater growth for the offspring of earlier spawning events. Older, and thus larger, fish may die after the first spawning event in a given season. Further, reproduction early in the season may be more important for population maintenance, and later spawning events may ensure against reproductive failure early in the spawning season (Durham & Wilde 2005). Typical survival rates for juveniles can reach 0.0048 but can drop nearly an order of magnitude with alterations in river discharge rates (Wilde & Durham 2008).

Environmental variation can also impact growth rates. In urbanized watersheds, Blacknose Dace grew faster in the first year of life and about 90% of individuals matured at age 1. In comparison only 25% of age-1 fish matured in less urbanized watersheds. The earlier maturation may be a function of higher ecosystem production and increased temperatures (Fraker et al. 2002).

Although most studies of digestive physiology have focused on European and Asian cyprinids, study of evacuation rates in a predaceous cyprinid, the Northern Pikeminnow, *Ptychocheilus oregonensis*, revealed relationships among prey volume, predator and prey weights, and temperature (Beyer et al. 1988). Cyprinids do not have a stomach (see morphology section) and do not produce hydrochloric acid or pepsin anywhere in the digestive tract (Hofer 1991). Northern Pikeminnows are large, carnivorous cyprinids that feed primarily on other fishes (Scott & Crossman 1973). Despite their lack of a true stomach, digestion in Northern Pikeminnows is similar to, or at least consistent with, that of piscivorous fishes with stomachs (Beyer et al. 1988). The species has a large, strong foregut, capable of powerful peristaltic movements. Volume of prey, rather than surface area, has the greatest impact on evacuation rate, but evacuation rate also was significantly dependent on and positively correlated with temperature, prey weight, and predator weight. Although temperature and prey weight could be manipulated to alter the evacuation rate by a factor of 3, predator weight accounted for only a 1.8 change in evacuation rate (Beyer et al. 1988).

Environmental Tolerance and Osmoregulation

Thermal Tolerances

Thermal biology, especially aspects such as the critical thermal maximum (CTM), is quite diverse among North American cyprinids. Thermal tolerances of minnows vary not only among species but also seasonally and geographically within species. CTM ranges from 25 to 35°C in most cyprinids, and to our knowledge, the highest reported CTM can be endured by the Smalleye Shiner, *Alburnops buccula*, at just over 40°C (Beitinger & Bennett 2000; Ostrand & Wilde 2001). CTM is seasonally variable in the Southern Redbelly Dace, *Chrosomus erythrogaster* (Scott 1987). Depending on the season, the CTM ranged from 17.5 to 32.3°C, a variation of >14°C. This variation in CTM was >60% of the seasonal ambient temperature range (21.5°C). In winter, the CTM of 17.5°C was lower than ambient summer water temps of 19–21.5°C. The Red Shiner, *Cyprinella lutrensis*, is abundant across the central United States and thrives in seemingly harsh habitats. Matthews (1986d) conducted a large-scale geographic study of the CTM over an 1,100 km north-south span of the range of the Red Shiner. No statistically significant geographic trends emerged in CTM, and thus, he hypothesized that CTM is conserved within the species. This is interesting in light of the findings on the Red Shiner that high thermal instability in some areas of the Brazos River, Texas (as a result of Sheppard Dam), corresponded to high genetic heterozygosity at the Mdh-B locus of Red Shiners and in significantly different proportions than Hardy-Weinberg equilibrium would predict (Zimmerman & Richmond 1981; see genetics section). This was interpreted as an adaptive response to the unstable temperatures of that area. Similarly, the preferred temperature of Red Shiners also is plastic and subject to selection (Calhoun et al. 1982). Though the Cyprinidae are not the most thermally tolerant group of fishes in North America, the range of CTM observed in the family is impressive, and the most tolerant cyprinids are more tolerant of high temperatures than most other North American freshwater fishes (Beitinger et al. 2000).

Salinity Tolerance

Cyprinids have long been classified as primary freshwater fishes (i.e., restricted to fresh water; Myers 1938). Salinity tolerances are fairly conserved within the family Cyprinidae; few species can tolerate any appreciable salinity. Most of these stenohaline fishes are not found in areas where salinity is >3 ppt (Young & Cech 1996). The Mojave Tui Chub, *Siphateles bicolor mohavensis*, shows increased tolerance of just over 10 ppt (McClanahan et al. 1986). Nevertheless, the Smalleye Shiner, *Alburnops buccula*, Sharpnose Shiner, "*Notropis*" *oxyrhynchus*, and Plains Minnow, *Hybognathus placitus*, have LC50 levels >15 ppt (Ostrand & Wilde 2001). This is higher than normal for members of this family. These heightened tolerances may help explain distributions and persistence in areas such as the Brazos River, Texas, where evaporation in pools can create temporarily increased salinities (Ostrand & Wilde 2001).

Even higher salinity tolerance is observed in two other North American cyprinids, the Splittail, *Pogonichthys macrolepidotus*, and the Peamouth Chub, *Mylocheilus caurinus*. Since these are sister-species (Simons & Mayden 1999), increased salinity tolerance likely was inherited from a common ancestor. Splittails can tolerate salinities of >28 ppt (Young & Cech 1996) and occur naturally in environments with salinities ≤18 ppt (Meng & Moyle 1995). Higher apparent sensitivity of young fish than adults to salinity may be a function of body surface area:volume ratio or incomplete development of the osmoregulatory system (Young & Cech 1996).

The curious distribution of the Peamouth Chub is the likely result of migration through brackish water (Clark & McInerney 1974). The species is native to rivers and lakes of the Pacific Northwest from the Columbia River, Oregon and Washington, north to the Nass River, British Columbia, including fjords that do not contain other primary freshwater fishes (Fig. 12.37). It is the only cyprinid species present on Vancouver Island off the coast of British Columbia. The species can move through brackish water and occurs in the sea off Spanish Banks, Vancouver, British Columbia (Carl et al. 1967). Their presence in areas that have no other cyprinids or primary freshwater fishes likely involved dispersal through brackish water during floods or other periods of high runoff. This dispersal may have occurred during glacial retreat at the end of the Pleistocene glaciations. The large amount of meltwater produced by glaciers may have created a brackish water corridor for migration.

Heightened salinity in fresh waters can cause stress to fish, altering other physiological parameters. Toepfer & Barton (1992) investigated the effect of salinity on oxygen consumption in the Southern Redbelly Dace, *Chrosomus erythrogaster*, compared with the Northern Studfish (*Fundulus catenatus*). The authors chose these taxa because the

Southern Redbelly Dace is not closely related to brackish or marine fishes, but the Northern Studfish is related to euryhaline species. At higher salinities (4 and 10 ppt) both species increased the rate of oxygen consumption, suggesting a higher metabolic rate. Nevertheless, the effects of salinity on Southern Redbelly Dace were significantly greater than those on Northern Studfish, suggesting that phylogenetic inertia plays a role in the osmoregulation and heightened metabolism of these fish.

Acidification Tolerance

Acidification of water bodies has become an important issue in recent years, especially as evidence mounts that acidification can be anthropogenic. Agriculture, air pollution, and other anthropogenic causes can acidify lakes and rivers, resulting in increased stress to fishes and other inhabitants. As lakes begin to acidify, the fraction of cyprinid species present is one of the first aspects of the ecosystem to change, which can make them good bioindicators of anthropogenic change to an ecosystem (Matuszek et al. 1990). Declining populations of Fathead Minnows, *Pimephales promelas*, Common Shiners, *Luxilus cornutus*, Bluntnose Minnows, *Pimephales notatus*, and Blacknose Shiners, "*Notropis*" *heterolepis*, are good indicators of declining ecosystem health as a result of anthropogenic acidification of lakes and rivers (Mills & Schindler 1986; Matuszek et al. 1990). The lower tolerance of minnows for acidity is typically pH 4–5 (Matthews & Hill 1977), which may be one explanation for their use as an early warning sign of acidification. Upper pH levels of nearly 11 can be tolerated by the Klamath Tui Chub, *Siphateles bicolor bicolor* (Falter & Cech 1991).

Turbidity Tolerance

Turbidity (suspended sediment particles in the water column) is another factor that can negatively affect minnows (e.g., foraging, reproduction), likely via respiratory or visual impairment (Vinyard & Yuan 1996; Sutherland & Meyer 2007; Hazelton & Grossman 2009). Minnows are among the most tolerant of fish groups to turbidity (Trebitz et al. 2007) but can still show signs of stress at even miniscule (25 mg/l) concentrations of suspended sediments (Sutherland et al. 2008). In a laboratory study of turbidity and competition effects, Rosyside Dace, *Clinostomus funduloides*, a species of clear, flowing streams, exhibited reduced reactive distance to prey (3.5 cm/10 nephelometric turbidity unit, NTU, increase, range 10–30 NTU) in turbidity, but turbidity interacted complexly with prey capture when trials included intra- and interspecific competitors (i.e., Yellowfin Shiners, *Alburnops lutipinnis*). Interestingly, the trials suggested increased turbidity decreased prey capture success forward of the fish's location, possibly representing an overall increase in energy costs associated with foraging (Hazelton & Grossman 2009), which could affect growth and overall fitness. Similarly, feeding trials with the Lahontan Redside, *Richardsonius egregius*, revealed a strong linear decrease in predation rates on zooplankton prey with even slight increases in turbidity (about 95% prey capture at 3.5 NTU to 20% at 25 NTU with 1.7 mm prey) (Vinyard & Yuan 1996). Turbidity decreases the effort that the Whitetail Shiner, *Cyprinella galactura*, invests in reproduction as well as the number of propagules spawned (Sutherland 2007). As is typical of other physiological tolerances mentioned here, minnows show diversity in their ability to tolerate turbidity. Comparative data for the Whitetail Shiner and Spotfin Chub (*Erimonax monachus*) show that Spotfin Chubs are less resilient to turbidity than Whitetail Shiners. Some authors suggest low turbidity tolerance of the Spotfin Chub is responsible for its declining numbers, leading to its Threatened status (Sutherland & Meyer 2007; Sutherland et al. 2008) (see also ecology and conservation sections).

Oxygen Tolerance

Low amounts of dissolved oxygen (hypoxia) also can negatively affect minnow species. As with other tolerance metrics discussed above, we know that a diversity of physiological requirements exists among species in this large clade, but we do not yet fully understand how physiologically diverse the clade is. The Red Shiner, *Cyprinella lutrensis*, can survive (though stressed) at dissolved oxygen levels between 0.9 and 1.5 ppm. Above that level, this species is not stressed. Red Shiners can survive (though stressed) for hours at <0.8 ppm dissolved oxygen (Matthews & Hill 1977). Other species such as the Plains Minnow, *Hybognathus placitus*, Arkansas River Shiner, *Notropis girardi*, and Emerald Shiner, *N. atherinoides*, lose equilibrium in <2 h at 1.5 ppm dissolved oxygen (Matthews & Maness 1979). Differences occur between headwater (i.e., intermittent, periodically low-oxygen conditions) and mainstream (i.e., continuous flow, unlikely to experience low-oxygen conditions) cyprinid species (Matthews & Styron 1981). Whether these are plastic effects of the environment or actual physiological tolerances of respective species is unclear. All tolerance levels examined were >1.0 ppm (Matthews & Styron 1981). In standardized assays (26°C trials) of 17 small stream cyprinid species, critical dissolved oxygen concentrations (measured as loss of equilibrium) averaged from 0.70 ppm in the Golden Shiner, *Notemigonus crysoleucas*, to 1.49 ppm in the Rosyface Shiner, *Notropis rubellus* (Smale & Rabeni 1995). Notably, 9 of the species showed critical values >1.0 ppm. In general, these oxygen requirements are not impressively high or low. For example, the Black Bullhead (*Ameiurus melas*) and Pumpkinseed (*Lepomis gibbosus*) can survive at dissolved oxygen levels much <0.8 ppm without loss of equilibrium (More 1942). Winter oxygen levels that are high enough for cyprinids to survive (about 1 ppm) provide a safe-haven for a cyprinid assemblage in northern bog lakes by excluding some predatory fishes (Rahel 1984).

Cyprinid Toxicology

Toxicological tolerances are well investigated within Cyprinidae with much emphasis placed on Fathead Minnows. As mentioned, this minnow is a favorite test subject of aquatic toxicologists, due in part to the ease with which it can be housed and bred, and also likely in part as a result of historical inertia. Researchers can compare work on the toxicology of a new compound to that of other compounds so long as they use the same species as a test subject. Unfortunately, this has led to a paucity of research comparing toxic effects on different species. Without that comparative knowledge, we cannot evaluate the effectiveness or accuracy of species such as the Fathead Minnow as an environmental indicator. Given the enormity of literature available, here we only introduce the topic by summarizing representative toxicological work on polychromatic hydrocarbons, several important major heavy metal pollutants, and toxins produced by cyanobacteria. We direct the interested reader to Ankley & Villeneuve (2006) for a more exhaustive review of the role Fathead Minnows play in understanding aquatic toxicology.

Fathead Minnows can show strong genetically based resistance to toxins, but even so, reproductive fitness often is ultimately affected. Fluoranthene is in a class of compounds called polycyclic aromatic hydrocarbons (PAHs), which are common pollutants from agricultural burning and the combustion of fossil fuels. Unexposed progeny of tolerant individuals of Fathead Minnows maintained high levels of tolerance, refuting the idea of physiological acclimation (Diamond et al. 1995). The concentrations tested were not sufficient to cause mortality in the fish but did lower reproductive capacity. Significantly fewer eggs (33%), lower hatch rate (21%), and lower larval survivorship (37%) occurred in exposed populations, resulting in a significantly reduced reproductive capacity in the exposed fish. Offspring had a 30% increase in resistance. Diamond et al. (1995) argued that although tolerance may confer some short-term benefits, long-term costs, such as lowered capacity to maintain viable population size and lowered genetic diversity, would ultimately lower adaptability to naturally fluctuating environmental conditions. Similarly anthracene, another PAH, affected reproductive potential of Fathead Minnows (Hall & Oris 1991). In this study, eggs were removed immediately after spawning, to reduce direct egg exposure to anthracene and examine the transferability of anthracene from mother to progeny. Exposed fish produced fewer eggs, and progeny from exposed mothers exhibited reduced hatching percentages and fry survival rates. Several mechanisms may account for decreased reproductive capacity, such as interference with reproductive behaviors, hormone receptor sites, and hormone production (Hall & Oris 1991).

The effects of heavy metal contamination also have been investigated in Fathead Minnows. Kolok et al. (2004) exposed Fathead Minnows to sublethal concentrations of copper and tested swimming performance. Swimming performance was tested before and after an initial exposure to copper; change in swimming performance after copper exposure was used as a proxy for tolerance to copper. After the swimming performance tests, the minnows were divided into two groups, one copper-tolerant and the other copper-susceptible. Fish were bred within each resistance regime, and the offspring tested for copper tolerance. The authors investigated allozyme heterogeneity as it related to tolerance, expecting that copper-tolerant parents would produce the most copper-tolerant offspring. Interestingly, although copper-tolerant parents did produce significantly tolerant offspring, so did copper-susceptible parents. The authors hypothesized that, since control groups were not exposed to copper before mating, the copper-tolerant and copper-susceptible individuals acclimated to the copper exposure and conferred that acclimated resistance to their offspring. This study demonstrates an important aspect of toxicology in general for minnows: acclimation can have a significant impact on tolerance, and acclimation can be transferred from parents to progeny. The mechanism for inheritance of acclimation is not understood.

Another heavy metal, mercury, is of great concern in many aquatic ecosystems due to bioaccumulation, in which animals higher on the food web concentrate mercury in their tissues. This can be hugely detrimental to top predators because sub-toxic levels observed in prey can accumulate to dangerous levels in predators. Webber & Haines (2003) investigated the effects of non-lethal dietary mercury concentrations on predator avoidance in Golden Shiners, *Notemigonus crysoleucas*. After exposure to dietary mercury over 90 days, they introduced a model avian predator and measured the responses of these fish. They observed heightened activity levels, greater (faster) vertical dispersal, and longer time to settling relative to controls. Those behaviors make the shiners more vulnerable to predation, thus accelerating the bioaccumulation of mercury in higher trophic levels. Mercury contamination also has been studied in the context of reproduction in Fathead Minnows. Drevnick & Sandheinrich (2003) exposed Fathead Minnows to three sublethal levels of dietary mercury and examined reproduction. Fish exposed to the highest concentration of mercury had a 0% spawning success rate, and the fish exposed to the middle concentration had a spawning success rate <50% of that for control fish. Mercury also had a significant impact on the hormones testosterone and estradiol in these fish and interfered with gonadal development, suggesting that hormone interference may hinder reproduction.

Selenium is another heavy metal that can detrimentally affect fishes. Selenium occurs naturally in low concentrations as a result of erosion from ore-bearing rocks. The environmental concentrations of selenium, however, can be increased greatly by anthropogenic activities such as combustion of coal and other fossil fuels, agriculture, industry, and mining operations. Female Fathead Minnows pass selenium to their progeny, and exposure can cause edema (overaccumulation of fluid in tissue spaces) and lordosis (unnatural curvature of the spine) (Schultz & Hermanutz 1990). Chronic selenium exposure and bioaccumulation cause serious detrimental effects on growth and development of the Splittail, *Pogonichthys macrolepidotus*, inhabiting the San Francisco Bay estuary (Teh et al. 2004; see conservation section). Dietary selenium concentrations were correlated inversely with growth. Spinal deformation and significant histopathological effects were observable after 9 months at only 6.6 μg selenium/g dry food weight. The high deformation rate (53.3%) at this level of exposure appeared to result from excessive lipid peroxidation. Interestingly, in the highest concentrations (26 and 57.6 μg/g dry weight) deformities did not occur at such a high rate, despite other effects such as lowered swimming activity and anorexia. The authors proposed that in order for selenium to exert its toxic effects (at least in the form of spinal deformities), metabolic activity must still be sufficiently high to metabolize the selenium into the form that causes the deformations and transports it to the tissues. At higher rates altered structural protein turnover and abnormal lipid metabolism resulted in either failure of the liver to metabolize the toxicant or failure to excrete the active forms throughout the body (Teh et al. 2004).

Acuña et al. (2012) investigated the potential effects of microcystins on the endangered Splittail, *Pogonichthys macrolepidotus*, in the Sacramento River (see conservation section). Microcystins are produced by the cyanobacterium *Microcystis*, which has exhibited seasonal blooms since 1999 in the Sacramento River system. Acuña et al. (2012) demonstrated sublethal effects in juvenile Splittails fed with microcystins at concentrations present in the environment. These effects include appearance of liver lesions, reduced RNA:DNA ratios suggesting reduced transcription rates, and inhibition of protein phosphatase 2A, all indicating liver damage. Their results suggest that *Microcystis* is toxic to the Splittail in the Sacramento River system and that environmental conditions producing cyanobacterial blooms will have negative effects on this Endangered species.

BEHAVIOR

Most studies of non-reproductive behavior of North American cyprinids focused on the anti-predator responses of Fathead Minnows. Behaviors of other species are not well documented or understood, in particular, enigmatic behaviors observed in the laboratory such as eye picking and oral grasping. These have not been observed in the field, and it is unclear if they are natural behaviors or artifacts of the laboratory environment.

Diel Activity

Most North American cyprinids are diurnal, although the Creek Chub, *Semotilus atromaculatus*, exhibits nocturnal reproductive behaviors (Maurakis et al. 1995). Some species will inhabit different habitats at night. For example, Red Shiners, *Cyprinella lutrensis*, move into shallow water at night (Yu & Peters 2002), while juvenile

Splittails, *Pogonichthys macrolepidotus*, inhabit shallow areas with emergent vegetation during the day but move to deeper areas with submerged vegetation at night (Sommer et al. 2008). Most cyprinids feed during the day; some species, such as the Central Stoneroller, *Campostoma anomalum*, Virgin Spinedace, *Lepidomeda mollispinis*, and Bluntnose Minnow, *Pimephales notatus*, feed continuously during the day (Moyle 1973; Fowler & Taber 1985; Angradi et al. 1991), but others such as the Speckled Dace, *Rhinichthys osculus*, and Mimic Shiner, *Notropis volucellus*, are more active at dawn and dusk (Moyle 1973; Angradi et al. 1991). During the summer, lake-dwelling Peamouth Chubs, *Mylocheilus caurinus*, move to the surface and inshore habitats at night and return to deeper water during the day (McPhail 2007). Diel movements can be on the order of 500 m in the Sacramento Pikeminnow, *Ptychocheilus grandis* (Harvey & Nakamoto 1999). These movements can be species dependent, even within the same stream. For example, the Bluehead Chub, *Nocomis leptocephalus*, moves at a rate an order of magnitude higher than the Rosefin Shiner, *Lythurus ardens* (Albanese et al. 2009).

Anti-Predator Behavior

Fathead Minnows exhibit anti-predator responses that include freezing, dashing, and increased use of shelter (Lawrence & Smith 1989). During freezing, fish sink to the substrate and remain immobile. Dashing consists of rapid, disoriented swimming that makes it difficult for a predator to track a target. Anti-predator responses can be induced by a variety of stimuli and depend on the experience and habitat of the individual fish. Fish exposed to predation in wild or natural habitats exhibit anti-predator responses when given visual or chemical cues (Mathis et al. 1993).

One of the most intensely studied intraspecific alarm cues is the Schreckstoff system found in otophysan fishes. This system consists of an alarm substance produced in the epidermis (Lawrence & Smith 1989; see physiology section). Most behavioral work on alarm cues is confined to a laboratory setting, but in one field study (Wisenden et al. 2004), alarm cues changed behavior of Blacknose Shiners, "*Notropis*" *heterolepis*. In the laboratory, naive individuals, or individuals that have not had the experience of association of alarm substances with predators, do not respond to visual or chemical cues (Mathis et al. 1993). Even so, they will respond to chemical cues if the predator has been feeding on conspecific minnows (Mathis & Smith 1993a; Mathis et al. 1993). Presumably, ingested alarm substance chemically labels predators (Matthis & Smith 1993b). Such labeling is present in the fecal matter of the Northern Pike (*Esox lucius*), a significant predator of Fathead Minnows (Brown et al. 1995a). Interestingly, the fecal matter of predators fed Brook Stickleback (*Culaea inconstans*), a non-ostariophysan that also produces alarm pheromones, also provoked an alarm response from Fathead Minnows. If the predator fed on Green Swordtails (*Xiphophorus helleri*), another unrelated fish that lacks alarm pheromones, no alarm response occurred. Brook Stickleback or Fathead Minnow alarm cues also are recognized by Fathead Minnows in the fecal matter of the Yellow Perch (*Perca flavescens*), Rainbow Trout (*Onchorynchus mykiss*), and Brook Stickleback (Chivers et al. 2002). Notably, behaviors associated with these reactions decreased the statistical probability of being captured by the predator. Interestingly, Northern Pike held in large tanks spent the majority of their time in the area of the tank where they were fed (in this case the food was dead Fathead Minnows), and defecated in a separate area of the tank. This suggests a behavioral adaptation of Northern Pike to counteract the anti-predator response of Fathead Minnows to fecal material containing alarm pheromone from previously consumed minnows (Brown et al. 1995b).

Anti-predator responses are learned rapidly. Naive wild populations of the Fathead Minnow showed anti-predator responses in <14 days of introduction of the Northern Pike into their environment (Chivers & Smith 1995b). Learning may be transmitted culturally (Chivers & Smith 1995a) as well as learned by experience. Alarm cues can be associated with visual or chemical indications of a predator (Chivers & Smith 1994ab). Affected fish can exhibit fright responses to either the scent of a predator alone or the sight of a predator alone so long as they have been exposed previously to the stimulus and conspecific alarm substances simultaneously.

Fathead Minnows also learn to react to alarm cues from other, non-cyprinid species. When raised in captivity with Brook Sticklebacks, Fathead Minnows can learn to respond to Brook Stickleback alarm cues so long as the minnows have been exposed to a predator and the Brook Stickleback alarm cue simultaneously, and Brook Sticklebacks are present in sufficient numbers (Pollock & Chivers 2004). Populations of Fathead Minnows that occur in sympatry with Iowa Darters (*Etheostoma exile*) responded to alarm cues from that species, but allopatric populations did not (Chivers et al. 1995).

Hunger also is correlated with alarm responses. When Fathead Minnows were deprived of food for 24 h, alarm responses were reduced significantly. After food deprivation, the behavior of Fathead Minnows exposed to alarm substance was not significantly different from that of control groups, illustrating a tradeoff between predator avoidance and foraging (Brown & Smith 1996).

The individual benefit of producing alarm substance has puzzled evolutionary biologists as the release of alarm substance would convey no benefit to a minnow that was mortally wounded or consumed by a predator. An individual fish benefits, however, if alarm substance release results in escape from a predator. Predators on Fathead Minnows, including the Northern Pike, are attracted to alarm substance and may be attracted to attempted predation events. Interference from a second predator during an attempted predation event may result in escape of the prey (Chivers et al. 1996), perhaps explaining in part the individual benefit of alarm substance.

Eye-picking Behavior

The unusual behavior of eye picking is known in one North American cyprinid. The Cutlips Minnow, *Exoglossum maxillingua*, has a highly modified lower jaw and, at least in captivity, uses this jaw to pick the eyes from other fish species (Scott & Crossman 1973; Page & Burr 2011). Whether this represents a specialized mode of feeding as noted in some Cichlids (e.g., Malawi Eyebiter, *Dimidiochromis compressiceps*) or if it is simply a response to crowded conditions is unknown. In one study of captive Cutlips Minnows, the removed eyes often were ingested, and eye picking increased in frequency under crowded conditions (Johnson & Johnson 1982). There are anecdotal accounts of eyeless fishes in streams (Johnson & Johnson 1982), but eye picking has not been observed directly in wild populations; diet studies suggest the Cutlips Minnow is primarily an insectivore (Johnson 1981; Jenkins & Burkhead 1994).

Oral Grasping

The behavior of oral grasping exists in several species of North American cyprinids in experimental settings. For example, Splittails, *Pogonichthys macrolepidotus*, can grasp an upstream screen when in a flume at mid- to high water velocities (Young & Cech 1996; Young et al. 2004). This behavior may be a metabolically efficient mechanism to maintain position during times of high water velocity and is perhaps used by juveniles in areas with flooded vegetation (Young et al. 2004). In other studies, nine species of cyprinids used oral grasping to maintain position in swimming experiments (Adams et al. 2000, 2003a): Blacktail Shiner, *Cyprinella venusta*; Bluntface Shiner, *Cyprinella camura*; River Shiner, *Alburnops blennius*; Longnose Shiner, *"Notropis" longirostris*: Weed Shiner, *Alburnops texanus*; Topeka Shiner, *Miniellus topeka*; Taillight Shiner, *"Notropis" maculatus*; Channel Shiner, *Notropis wickliffi*; Silver Chub, *Macrhybopsis storeriana*; and Fathead Minnow. Oral grasping occurred at about 70–80% of maximum swimming speed of these species. This behavior may be an effort to maintain position during periods when water speeds and durations exceeded aerobic swimming ability and also might result from fatigue (Adams et al. 2003a). The grasps usually were maintained for only a few seconds (Adams et al. 2003a) and have never been observed in the wild.

Larval Behavior

Little is known of larval behavior in North American cyprinids. Most are likely diurnal feeders. Several riverine species exhibit nocturnal drift behavior, moving up in the water column at night to be carried downstream to rearing areas. This has been observed in larvae of the Peamouth Chub, *Mylocheilus caurinus*, and Northern Pikeminnow, *Ptychocheilus oregonensis*, in the Columbia River (Gadomski & Barfoot 1998) and the larvae of several species of Great Plains cyprinids (Muth & Shmulback 1984; Platania & Altenbach 1988). Presumably the adults or subadults subsequently migrate upstream.

Learning

Golden Shiners, *Notemigonus crysoleucas*, are schooling cyprinids and forage widely within the water bodies they inhabit. Golden Shiners can learn time-place associations (Reebs 1996) and will also learn from other individuals. In experimental situations, groups of naive individuals that exhibit little movement in a tank will follow experienced individuals to food. Thus, actions taken by a minority of individuals have the potential to impact the behavior of the entire group (Reebs 2000).

REPRODUCTION

Reproduction in North American cyprinids is complex, reflecting the diversity of this group. As might be expected from such a large group of organisms inhabiting a wide range of aquatic environments, reproductive modes, fecundity, and egg characteristics vary substantially (Tables 12.2–12.5). Here we summarize seasonality, spawning cues, and fecundity in North American cyprinids. We then describe the modes of reproduction observed in these fishes, discuss adaptive hypotheses of nest association and the evolution of these spawning modes, and close with descriptions of egg characteristics, sexual maturity, and sexual dimorphism.

Seasonality

Most species of North American cyprinids have extended reproductive seasons, usually beginning in spring and extending through summer. Many species spawn as early as May with reproductive seasons >8 months for the Weed Shiner, *Alburnops texanus* (Heins & Rabito 1988), Longfin Dace, *Agosia chrysogaster* (Minckley & Barber 1971), and Bannerfin Shiner, *Cyprinella leedsi* (Heins & Rabito 1986). The Golden Shiner, *Notemigonus crysoleucas*, spawns as late as December in some parts of Florida (McLane 1955). Longfin Dace spawn in the southwestern United States from December to July. In contrast, Northern Pikeminnows, *Ptychocheilus oregonensis*, spawn only in June and July (Patten & Rodman 1969). Seasonality may govern reproduction in prairie stream cyprinids such as the Arkansas River Shiner, *Notropis girardi*, Peppered Chub, *Macrohybopsis tetranema*, Plains Minnow, *Hybognathus placitus*, Flathead Chub, *Platygobio gracilis*, and Red Shiner, *Cyprinella lutrensis*, by way of stream discharge, which is hugely important in reproductive success (Durham & Wilde 2006).

Spawning Cues

Spawning cues include seasonal, pheromonal, auditory, and visual communications. Both photoperiod and temperature play key roles in spawning and gonadal phenology (de Vlaming 1975). Pheromones are thought to function as a mode of recognition of individuals, sex, and species; however, they are best known for their function in coordination of spawning efforts within a species (Stacey & Sorensen 1991). Spawning in many fish species is thought to be influenced by pheromonal cues; however, these processes have only been intensely studied in the Goldfish and Zebrafish, but not in any native North American cyprinids (e.g., Stacey & Sorensen 1991; Sorensen & Scott 1994; Stacey et al. 1994; Bjerselius et al. 1995).

Pheromonal cues are not the sole mode of intraspecific reproductive signaling in cyprinids. Species of *Cyprinella* (Stout 1975; Phillips & Johnston 2008ab, 2009; Phillips et al. 2010; Fig. 12.76c) and *Pimephales* (Johnston & Johnson 2000) produce sounds during the breeding season. Though male Bluntnose Minnows, *Pimephales notatus*, produce sounds associated with aggressive behaviors, whether sounds are used during courtship or the spawning act remains unclear (Johnston & Johnson 2000). Male Satinfin Shiners, *Cyprinella analostanus*, produce three main types of sounds: single knocks, rapid knock series, and purrs (Stout 1975). Single knocks are produced when a male is chasing another male. Rapid knocks in series are produced when breeding males fight. When recordings of these sounds are played to fish in the laboratory, they stimulate the activity of the dominant male. Purrs, which are produced during mating, stimulate the courtship behavior of males and stimulate the female to remain near the sound-producing male. These sounds are complex with fourteen variables needed to completely describe the diversity of sounds produced by Whitetail Shiners, *C. galactura* (Fig. 12.76c); all species of *Cyprinella* probably produce sound during male-male interactions or male-female interactions, though only a few have been studied (Delco 1960; Phillips & Johnston 2008ab, 2009; Phillips et al. 2010).

The bright nuptial colorations of many cyprinid species suggest that visual cues are important for mate recognition and spawning (Figs. 12.76, 12.79–12.82), but visual cues have not been studied intensively. Other visual cues, such as male dry spawning passes (i.e., no milt released), are also thought to act as intraspecific spawning cues.

Fecundity

Fecundity is relatively high but variable in North American minnows (Tables 12.2–5). Some species, such as the Orangefin Shiner, "*Notropis*" *ammophilus*, and Taillight Shiner, "*N.*" *maculatus*, lay between 100 and 320 eggs/year (Etnier & Starnes 1993). Others, such as the Spotfin Shiner, *Cyprinella spiloptera*, Red Shiner, *C. lutrensis*, Mississippi Silvery Minnow, *Hybognathus nuchalis*, and Creek Chub, *Semotilus atromaculatus*, may lay >7,000 eggs in a single season (Etnier & Starnes 1993). A single female Red Shiner, *Cyprinella lutrensis*, laid >113,000 eggs in a 21-month laboratory test under 24-h light conditions (Gale 1986). Most species of minnows lay 800–1,500 eggs/season (Etnier & Starnes 1993). Variation in fecundity is not only observed in distantly related species. Bluntnose Minnows, *Pimephales notatus*, lay 200–500 eggs/season (Hubbs & Cooper 1936), and a close relative, the Fathead Minnow, *P. promelas*, lays 4,000–5,000 eggs/season (Markus 1934). A female Fallfish, *Semotilus corporalis*, contained >12,000 eggs immediately before spawning (Reed 1971).

Broadcast and Crevice Spawning

Spawning modes in cyprinids are diverse and interconnected. Some cyprinids prepare the substrate for spawning, but others do not. Those species with no substrate preparation have two spawning modes: broadcast spawning and crevice spawning. Broadcast spawning is considered the ancestral state for breeding in cyprinids (Page & Johnston 1990ab; Mayden & Simons 2002). This mode involves scattering of gametes over the substrate and occurs in most species of North American minnows (Johnston & Page 1992; Tables 12.2–2.5). Six species in the Rio Grande (*Hybognathus placitus*, *Hybognathus amarus*, Rio Grande Silvery Minnow, *Macrhybopsis aestivalis*, *Notropis girardi*, *Notropis jemezanus*, Rio Grande Shiner, and "*Notropis*" *simus*, Bluntnose Shiner) compose a reproductive guild of pelagic broadcast spawners. During increases in stream flow, these pelagic spawners broadcast semi-boyant eggs that remain suspended in current during development (Dudley & Platania 1999). Several species of cyprinids are nest associates, spawning over the nests of other fishes (see nest associates subsection).

In general, broadcast-spawning males do not occupy territories (Raney 1939a). In the Northern Pikeminnow, *Ptychocheilus oregonensis*, groups of ≤8,000 individuals (males outnumbering females 50M:1F to 200M:1F) congregate and swarm over coarse gravel where spawning occurs (Patten & Rodman 1969). Most groups of broadcast spawners are not nearly as large. Generally, a female and one to several males will break away from the spawning swarm, and one male clasps the female. Sperm and eggs are released by the pair and the surrounding males. In the Spikedace, *Meda fulgida*, the spawning group (one female and one to several males) makes abrupt vertical dashes during the spawning act, led by the female, touch the surface of the water, and then make a steep dive toward the substrate. Some members of the group actually touch the substrate (Barber et al. 1970). In some broadcasting cyprinids, such as the Eastern Blacknose Dace, *Rhinichthys atratulus*, the pair vibrates during spawning while resting on the substrate, which can result in burying of the eggs (Johnston & Page 1992).

Crevice spawning occurs in four genera: *Cyprinella*, *Codoma*, *Erimonax*, and *Tampichthys*. Here we describe reproduction in *Cyprinella* (Fig. 12.76cd), although our description is consistent with accounts of *Codoma*, *Erimonax*, and *Tampichthys*. Male *Cyprinella* defend territories over submerged logs with loose bark, fissures in large rocks, spaces between adjacent rocks, or other crevices for egg deposition (Pflieger 1965; Gale 1986; Mayden & Simons 2002). The males are tenacious defenders of their territories. Territorial male Spotfin Shiners, *C. spiloptera*, defend their respective crevices using their mouths to grab threatening males by the pelvic or anal fins and drag them away from the crevice area (Gale & Gale 1977). Males display by making passes across the crevices and leading females to the territory (detailed by Stephens & Mayden 1998; Mayden & Simons 2002). Male Spotfin Shiners usually extend a pectoral fin into the crevice while making these display passes (Gale 1986). A female enters the territory, and the pair swims together through the crevice with their vents oriented toward the crevice, vibrating during the spawning act itself as the eggs are deposited into the crevice (Fig. 12.76d). This may be repeated several times by the same pair before the female leaves. Males may mate with multiple females, and spawning crevices may be used sequentially by multiple males.

Substrate Preparers, Clumpers, and Clusterers

Many species of cyprinids practice careful preparation of the substrate before breeding. About 8% of North American minnows build nests for spawning not including crevice, clump, or cluster spawners (Johnston 1989). Species that prepare the substrate can build saucer-shaped, pit, and ridge nests with pits traversing the ridges. Others build gravel mounds, and some species clump or cluster their eggs in specific pre-cleaned cavities. In North American cyprinids, only the male prepares spawning sites.

Saucer building occurs only in the Longfin Dace, *Agosia chrysogaster* (Minckley & Barber 1971). Males construct and maintain large, saucer-shaped depressions on sandy substrates. These depressions can occur in relatively high densities, 25/m^2, and can reach 25 cm in diameter and 6 cm in depth. A rim around the saucer extends about 1 cm above the substrate. Males do not seem to defend territories, although they will display while over a nest.

In spawning, one to four males align next to a receptive female, but only one or rarely two actually mate with her. The pair or trio vibrates close to the substrate during gamete release and raise a cloud of silt that buries the eggs. After spawning is complete, neither parent guards the nest or provides any parental care.

Members of *Campostoma* and some members of *Luxilus* spawn in pits that males dig in gravel. Males move gravel aside with their snouts and mouths (in *Campostoma*). In some cases, *Luxilus* males (Figs. 12.76ab and 12.81) will breed as nest associates with species of *Nocomis* (see nest associate subsection). The pits are generally shallower than the saucer depressions of male *Agosia*. Though male *Campostoma* defend territories (Fig. 12.77c), they often switch between pits. The dominant male positions himself on the upstream edge of the pit; groups of females stay outside of the pits, entering individually when ready to spawn. Once a female enters the pit, one or more males align with her, they all vibrate, and gametes are subsequently released (Miller 1962). Species of *Campostoma* also spawn over nests of other cyprinids as nest associates (see nest associates subsection) (Fig. 12.77b). Within *Luxilus*, at least three members (Common Shiner, *L. cornutus*, Duskystripe Shiner, *L. pilsbryi*, and Bleeding Shiner, *L. zonatus*) nest in pits. Several other species (Crescent Shiner, *Luxilus cerasinus*, Warpaint Shiner, *L. coccogenis*, White Shiner, *L. albeolus*, and Bandfin Shiner, *L. zonistius*) spawn as nest associates. Pit-digging males defend territories and display over the pits for females. When a female enters the nest, the male tilts to one side; the female lays on the substrate. The male then clasps her with his curved body and pushes her into the substrate. Upon vibration, the pair releases gametes and departs (Gleason & Berra 1993; Maurakis & Woolcott 1993).

Perhaps the most peculiar reproductive mode in North American minnows is the pit-ridge building by male *Semotilus*. In these fishes, males construct nests in about 0.5 m of water (Ross & Reed 1978). A male excavates a pit in the gravel substrate and piles all of the excavated stones directly upstream of the pit. Males can move individual stones weighing ≤168 g in the excavation process (anecdotal accounts suggest weights of 500 g). An entire nest can weigh ≤80 kg (Reed 1971); *Semotilus* males rarely reach 1.6 kg in body weight. A receptive female can apparently only enter the nest area when the nest-building male is distracted by chasing another fish or building the nest itself, or he will chase her out as well (Ross 1976). Once over the nest pit, the male clasps the female by placing his pectoral fin under her anterior ventral surface and his caudal peduncle over her dorsal surface, twisting his body into a U shape. The female is forced into a nearly vertical position with her tail pointed toward the substrate immediately before gamete release. After the spawning bout is finished, the female typically floats belly up with the current for a short distance. She then proceeds to mate again with either the same or another male. Male Fallfish, *Semotilus corporalis*, do not use a spawning clasp. As a result, access to the female is not monopolized by a single male, and sneaker males, non-nest-building mature males who attempt copulation on other males' nests, are common (Ross & Reed 1978). Immediately after spawning, the male covers the pit (and eggs) with rocks from the downstream edge of the pit. As he continues to spawn, the pit is moved farther and farther downstream with the gravel from the downstream edge of the pit moved to the upstream edge. In this way, a ridge forms as successive spawning pits are filled. This ridge can be >2 m in length and 0.6 m in height (Reed 1971), an impressive feat for a species whose maximum recorded length is 0.5 m (Page & Burr 2011). The male guards the nest aggressively against other males and potential predators until hatching (Reed 1971; Ross 1977a; Johnston & Page 1992). On occasion, a large male may challenge the nest-building male, and the two begin a rapid upstream parallel swim. During this 1- to several meter swim, the males periodically push against each other. Finally, the winning male swims back to the nest, and the losing male swims away. This parallel swim as well as lateral displays and head butting are used to establish a hierarchy among the breeding males in a population (Ross 1977ab). About 10% of mature males build nests in any given year; the remaining males either do not spawn or act as sneaker males, stealing chances to mate with a female on the nest of another male. Interestingly, despite their aggressive territoriality, guarding males tolerate Blacknose Dace, Striped Shiners, *Luxilus chrysocephalus*, Common Shiners, *L. cornutus*, Blackside Dace, *Chrosomus cumberlandensis*, and White Suckers (*Catostomus commersoni*), all of which are known nest associates of *Semotilus* (Ross 1977a; see nest associates subsection; Fig. 12.56g). Males may use the same spawning site within and among spawning seasons (Ross & Reed 1978).

Species in the genera *Nocomis* and *Exoglossum* are mound builders in which males build large mounds of gravel with their mouths in slow- to moderately flowing water (Lachner 1952; Raney 1939b; Van Duzer 1939). A single male builds a nest about 0.5 m in diameter out of pebbles brought from ≤25 m from the nest (Fig. 12.78). If uninterrupted, a male can build the nest in a single day.

Multiple males can work simultaneously on the same nest (Johnston 1991). Mound construction consists of four stages: a cavity is excavated; a platform 0.5 m in diameter is built over the excavation; a mound is constructed over the platform; and finally, small pits or troughs are dug by the male on top of the mound (Maurakis et al. 1991a; Johnston & Page 1992). Hornyhead Chub, *Nocomis biguttatus*, mounds can consist of a collection ≤300 pebbles, with a combined weight of 11 kg (Wisenden et al. 2009b). Males clasp females by placing the pectoral fin on the ventral side of the female and the caudal peduncle on the dorsal side of the female. On occasion two males clasp the same female simultaneously (Maurakis et al. 1991a); satellite or sneaker males may fertilize eggs before the nest-building male (Sabaj et al. 2000). Male Central Stonerollers, *Campostoma anomalum*, may accompany a female Bluehead Chub, *Nocomis leptocephalus*, and get caught in the spawning clasp of a male Bluehead Chub (Fig. 12.78ab; Sabaj et al. 2000). Aside from these anomalous occurrences, generally a single male will guard his nest against other males. Males in *Nocomis* generally cover the eggs with gravel after spawning and continue to guard the nest until hatching (Johnston 1991).

Egg clustering coupled with intense parental care occurs only in *Codoma*, *Pimephales*, and *Opsopoeodus* (Gale 1983; Page & Ceas 1989; Minckley & Vives 1990; Page & Johnston 1990a; Mayden & Simons 2002; Table 12.4ac). Spawning in these fishes is initiated when a male establishes a territory under a horizontally flattened rock (or perhaps another solid surface). In Pugnose Minnows, *O. emiliae*, males rapidly raise and lower the dorsal fin immediately before spawning occurs. The guardian male lines up broadside and head-to-head with the female, and the pair makes several passes under the rock, laying and fertilizing several eggs during each spawning pass (Page & Johnson 1990a). Egg deposition in *Pimephales* involves females attaching eggs to the nest-stone with a rapid lateral undulation; the male uses his body to press the female's side against the roof of his territory, where she deposits the eggs (detailed by Page & Ceas 1989). The male remains in his territory, and several females may sequentially mate with him, leaving the eggs in his care. Males will continue to guard eggs until they hatch.

Spawning Mode and Male-Male Competition

Given such a high diversity of spawning behaviors, one would expect some spawning modes to show greater male-male competition than other modes. Pyron (2000) hypothesized that due to greater sperm competition between males of spawner groups (i.e., broadcast, saucer building) compared with pair-wise spawners (i.e., egg clustering, pit building, mound building), the former would have a greater testes:body mass ratio. Nevertheless, no significant differences were detected in regressions of testes mass against body mass for species with different spawning modes. The influence of spawning mode on male-male competition is not yet fully resolved.

Nest Associates

Many species of minnows, especially broadcast spawners, are nest associates, using the nests of other fishes, usually species of *Nocomis* (Figs. 12.77b and 12.78) or Sunfishes (Centrarchidae). Nest association is known in only three non-cyprinid taxa: Gars (Lepisosteidae) (Goff 1984), Lake Chubsuckers (*Erimyzon sucetta*), and Creek Chubsuckers (*Erimyzon oblongus*) (Page & Johnston 1990b). Interestingly, the Creek Chubsucker will breed over nests constructed by Central Stonerollers, *Campostoma anomalum*, and Creek Chubs, *Semotilus atromaculatus*.

Most species of nest-associating minnows spawn on nests constructed by other cyprinids, but some minnow taxa spawn in non-cyprinid nests. Golden Shiners, *Notemigonus crysoleucas*, spawn over active nests of Largemouth Bass (*Micropterus salmoides*) and may account for ≥78% of all eggs in the nest (Kramer & Smith 1960). Bluehead Shiners, *Pteronotropis hubbsi*, Bluenose Shiners, *P. welaka*, Golden Shiners, *Notemigonus crysoleucas*, Dusky Shiners, *Hudsonius cummingsi*, and three species of *Miniellus* (Topeka Shiners, Swallowtail Shiners, and Dusky Shiners) spawn over centrarchid nests (Carr 1946; Chew 1974; Noltie & Smith 1988; Fletcher & Burr 1992; Johnston & Page 1992; Fletcher 1993; Shao 1997ab; Johnston & Knight 1999; Boschung & Mayden 2004). Redfin Shiners, *Lythurus umbratilus*, spawn over Green Sunfish (*Lepomis cyanellus*) nests (Hunter & Wisby 1961). Odors from milt and ovarian fluids are the primary attractant of Redfin Shiners to the nests of Green Sunfish, rather than the nest itself (Hunter & Hasler 1965). In all these cases, the centrarchids only rarely chase off the minnow species, although the nests are guarded vigorously by the male Sunfish from other species of fishes, especially other centrarchids.

In several species of *Luxilus*, the nests of Bluehead Chubs, *Nocomis leptocephalus*, are used as a spawning substrate without modification. The White Shiner, *L. albeolus*, however, does alter the nest slightly; males dig furrows in the nest (about the length of the male) using their snouts. The male holds a territory around the furrow and waits for a receptive female. Male Crescent Shiners, *Luxilus cerasinus*, in contrast, do not dig furrows but still maintain territories on the mound (Maurakis & Woolcott 1993). The Rainbow Shiner, *Alburnops chrosomus*, and the Rough Shiner, *A. baileyi*, also spawn in depressions in the nests of the Bluehead Chub; however, they use pre-existing depressions in the nest rather than creating them (Johnston & Kleiner 1994). These behaviors are typical of many nest-associating minnows, such as the Yellowfin Shiner, *A. lutipinnis* (McAuliffe & Bennett 1981; Wallin 1989), and Bandfin Shiner, *L. zonistius* (Johnston & Birkhead 1988).

Advantages and Disadvantages of Nest Association

Since nest association is common in North American minnows, it clearly confers some advantages to the associate. Surprisingly, even potential predators of the nest associate can occasionally serve as host to nest-associating minnows. Bowfin, *Amia calva*, which typically prey on minnows and other small fishes, can act as host to Golden Shiners, *Notemigonus crysoleucas*, and it is unknown why the host fish do not consume the spawning minnows or their offspring (Katula & Page 1998). The association of the Dusky Shiner, *Hudsonius cummingsae*, is verifiably detrimental to its host, the Redbreast Sunfish (*Lepomis auritus*), because the shiner actually consumes the host's eggs (Fletcher 1993). Egg-eating leeches can occur in spawning nests that would presumably consume host and associates alike, thus encouraging hosts to allow associate spawning (Light et al. 2005). This mutualistic dilution has been argued as an explanation for protection in multiple host species (Johnston 1994; Shao 1997). Nest association can also cause direct hybridization in some minnow species (Scribner et al. 2000).

Nest association in North American minnows has evolved several times with several hosts (Johnston & Page 1992; Mayden & Simons 2002). Invasive, non-native nest associates are competitively excluded from prime spawning sites by native nest associates (Herrington & Popp 2004), which is indicative of the tight coupling of host and associate. The precursor to nest association likely is broadcast spawning, although some species, such as members of *Campostoma*, are known nest associates but generally construct pits for spawning, suggesting plasticity in spawning mode. Several theories attempt to explain the selective pressure driving a shift to nest association as well as the selective pressure on the host species to allow for nest associates to mate over the nest (Johnston 1991). One obvious advantage to the associate is parental care without parental investment. The associate can deposit eggs on clean, well-aerated substrate, and the nest receives protection against predators from the host (Shao 1997). The associate parents do not invest any effort in either preparation of the substrate or protection of the eggs or fry after spawning. According to the selfish-herd hypothesis (Hamilton 1971), nest association could increase survivorship because eggs of the associate are less likely to be eaten by egg predators because other eggs are also available. McKaye (1981) discussed mutual benefits of group spawning aggregations in his adaptive or mutualistic hypothesis. He described how, unlike brood parasites such as birds (e.g., cuckoos, Cuculidae), the alien or associate young do not remove or displace the host young, attacks by predators lead to only partial loss of brood (arguably less than without the associate brood), and the extra energetic input by the host species needed is low or nonexistent.

Nests could also act to synchronize spawning events. For example, the Redfin Shiner, *Lythurus umbratilus*, is attracted to the milt and ovarian fluid of the Green Sunfish (*Lepomis cyanellus*) with which it is a nest associate. This olfactory attraction, rather than the physical nest itself, should attract minnows from greater distances, resulting in a widespread signal of breeding time and location (Hunter & Hasler 1965; Johnston & Page 1992). The use of host species' milt to induce spawning in the associate Blackside Dace, *Chrosomus cumberlandensis*, has allowed for captive breeding that is otherwise impossible in this species (Rakes et al. 1999).

Another interesting issue of nest associate recognition is that, although hosts with nest associates voraciously guard their nests from potential predators, nest associates are not chased away (e.g., Kramer & Smith 1960; Hunter & Wisby 1961; Ross 1977a). One possible explanation is that males of the host species may be energetically incapable of driving away nest associates (Johnston 1991). The defense of the nest may simply come to a point of diminishing returns; protection afforded the nest by chasing away potential spawning associates is negligible when compared with the protection with that energy focused on chasing away potential egg predators.

Evolution of Spawning Modes

As noted, broadcast spawning generally is accepted as the plesiomorphic mode in North American minnows (Johnston & Page 1992) as well as in the shiner clade (Mayden & Simons 2002). Evidence indicates crevice spawning evolved directly from broadcast spawning (Johnston & Page 1992; Mayden & Simons 2002). This evolutionary shift occurred independently at least three times in the shiner clade alone (Mayden & Simons 2002). Pit building is most likely derived from broadcast spawning as well, but the ancestral state of saucer building in *Agosia* is equivocal (Mayden & Simons 2002). Pit-ridge building in *Semotilus* may be derived from pit building (Johnston & Page 1992). Differences in behavior suggest two separate origins of mound building for *Nocomis* and *Exoglossum*; *Exoglossum* does not perform the initial excavation stage seen in *Nocomis* (Johnston & Page 1992).

Egg clustering, observed in *Codoma*, *Opsopoeodus*, and *Pimephales*, is hypothesized to be derived from crevice spawning due to the relative similarity of those spawning modes (egg attachment, male territorial behavior, and male parental care) as opposed to broadcast spawning (Johnston & Page 1992). Nevertheless, phylogenetic support for this hypothesis is weak, and the ancestral state for the derivation of egg clustering is, at best, equivocal (Mayden & Simons 2002).

Without greater taxon sampling, phylogenetic resolution, and intense study of reproductive behaviors, theories on the evolution of reproductive modes will remain speculative, especially due to the homoplastic nature of many of these behaviors. In addition, categories such as "broadcast spawning" likely need further subdivision (e.g., broadcast spawning with and without male territoriality), all of which have not been sufficiently investigated. One major difficulty with several studies of the evolution of spawning mode is that they were not conducted with reference to a well-resolved, explicit phylogenetic hypothesis because none were available. Use of reproductive characters alone to understand their evolution will underestimate the number of independent origins of a particular behavior. An understanding of the evolution of spawning mode will only be reached when investigated in the context of other phylogenetically informative characters.

Egg Characteristics

Many minnow species spawn multiple clutches (Heins & Rabito 1986; Johnston & Kleiner 1994). Heins & Rabito (1986) defined a clutch as comprising propagules that undergo synchronized development and observed multiple events of synchronous development in a single season in two species of minnows from the genus *Alburnops*. Clutch size often is correlated with female length (Heins & Baker 1992; see also Haag et al. 2007). Stream runoff significantly is correlated with egg size (after correcting for body size) in the Blacktail Shiner, *Cyprinella venusta*, such that high runoff appeared to select for larger egg size in these minnows (Machado et al. 2002). In this case, egg size and clutch size were unrelated. In contrast, an apparent tradeoff occurred between clutch size and egg size in the Weed Shiner, *Alburnops texanus*, with larger eggs (and decreased clutch sizes) being associated with higher mean annual runoff in the Gulf Coastal Plain (Heins & Rabito 1988). Even within the Gulf Coastal Plain, large (<300%) variation occurs in the weight of mature oocytes (Heins & Baker 1987). In another species, the Yazoo Shiner, "*Notropis*" *rafinesquei*, ova sizes (and many other reproductive traits) varied significantly among females in three abundant populations despite their close geographic proximity. The highly plastic nature of reproductive traits in this species (and close relatives) likely is an important adaptation allowing the Yazoo Shiner to maintain large populations in the often physically unstable and unpredictable stream environments of the Gulf Coastal Plain (Haag et al. 2007).

Eggs are adhesive and stick to the spawning substrate in *Pimephales* and other egg-clustering minnows (Page & Ceas 1989) but are non-adhesive and unattached in species whose eggs are laid on mound nests such as *Nocomis* and *Exoglossum* (Van Duzer 1939; Lachner 1952) and broadcast spawners such as the Eastern Silvery Minnow, *Hybognathus regius* (Raney 1939a). Cyprinid eggs can hatch in <4 days in optimal conditions (Minckley & Barber 1971), and time to hatching is influenced strongly by temperature (Tables 12.2–12.5).

Sexual Maturity and Sexual Dimorphism

North American cyprinids are never reproductively active in the first summer of life, though in some populations, animals at age 1+ (i.e., the second summer of life) can be reproductively active. Although somewhat variable, sexual maturity in most minnow species is reached in either the second or third summer (age 1+ and age 2+, respectively), though Fallfish, *Semotilus corporalis*, females may not be sexually mature until their fourth year (Reed 1971). Higher runoff is correlated with increased size at sexual maturity of a cyprinid fish (Weed Shiner, *Alburnops texanus*) in the Gulf Coastal Plain (Heins & Rabito 1988), but no cause and effect mechanism was ascertained.

The appearance of nuptial structures such as tubercles, enlarged fins, changes in coloration (which are often bright reds, yellows, blues, and greens in breeding males), sexual size dimorphism, and nest-building behavior are all indicators of sexual maturity. Evolutionary shifts to sexual dimorphism are concentrated in lineages where shifts to male guarding and sperm competition occur (Pyron 1996). This dimorphism underscores the role of the male as guardian of the nest as noted in the previous discussion of nesting.

ECOLOGY

Cyprinids often dominate stream communities in taxonomic diversity, number of individuals, and biomass. Thus, they likely have a strong influence on ecosystem structure and function. Due in part to their relative abundance and size, they form fundamental links in many food webs. Most studies of ecology of North American cyprinids are descriptions of the ecology and life history of single species, often those that are Threatened or of Special Concern. Here we focus on studies that address broader topics of spatial and trophic ecology. We also include a discussion of the functional impact that cyprinids have in ecosystems, in terms of both biotic shifts and nutrient cycling, and conclude with an overview of host-parasite relationships. We do not describe all ways in which minnows interact with other species and their environment (such a task would fill a volume by itself!) but instead highlight examples of habitat use, the diversity of predator-prey relationships, and the impact of these interactions on the dynamics of North American aquatic ecosystems.

Spatial Ecology

The distribution of minnows within and among environments is a function of their phylogenetic history (Mayden 1987) and environmental requirements. Aside from physiological factors determining spatial distribution (see physiology section), ecological interactions with other species typically determine distribution patterns, and feeding patterns (e.g., which particular species an insectivore consumes) are highly correlated with where these organisms spend the majority of their time (Mendelson 1975). Habitat preferences manifested in the absence of competitive heterospecifics can be swamped out when interspecific interactions are strong (Gorman 1988a). Distributions can be patchy or uniform across microhabitats within a stream, different groups can stratify based on a variety of factors, and most cyprinids engage in schooling behavior during some stage in their lives. Most of these patterns are likely due to ecological interactions between species, often predatory ones.

One prediction derived from the theory of habitat distribution (Fretwell 1972) is that populations become distributed more uniformly over habitat patches as population size increases. Blacknose Dace, *Rhinichthys atratulus*, and juvenile Creek Chubs, *Semotilus atromaculatus*, conform to this prediction (Fraser & Sise 1980); however, in the same stream, adult Creek Chubs remained clumped, even at high population sizes. This difference is likely due to differences in trophic ecology. Blacknose Dace and juvenile Creek Chubs feed on invertebrates, but adult Creek Chubs are largely piscivorous (Cerri & Fraser 1983). Clustering around shelter may increase their success as ambush predators. The presence of large predators (adult Creek Chubs) also determined habitat use by Blacknose Dace and juvenile Creek Chubs (Fraser & Cerri 1982).

Minnows often segregate by species or life stage vertically and horizontally, but positive spatial interactions also occur among heterospecifics. Differences in food use are often governed by differences in this type of space use (Mendelson 1975). In Mississippi, vertical position and vegetation were the two best predictors of spatial resource partitioning within an assemblage of small-stream cyprinids (Baker and Ross 1981) despite considerable interspecific overlap in space. In a microhabitat study of five Ozarkian cyprinid taxa (Central Stoneroller, *Campostoma anomalum*, and Largescale Stoneroller, *C. oligolepis*, combined; Bleeding Shiner, *Luxilus zonatus*, Figs. 12.56h, 12.80; Hornyhead Chub, *Nocomis biguttatus*; Bigeye Shiner, “*Notropis*” *boops*; and Ozark Minnow, “*Notropis*” *nubilus*), species also segregated vertically, and their relative positions remained constant with changes in depth (Gorman 1987). This assemblage used virtually all habitat space, supporting the hypothesis that resource use should approximate the distribution of available resources (Sale 1974; Lawlor 1980). Habitat use is typically dynamic and dependent on configuration of the habitat and interactions with heterospecifics, but positive interactions may facilitate opportunistic feeding. Positive heterospecific interactions such as schooling may serve as an anti-predator tactic. Young-of-the-year Hornyhead Chubs, Ozark Minnows, and *Campostoma* spp. segregated horizontally from adults, and the adults avoided shallower water in pools and raceways. Presumably this minimizes competition with adults and predation by large-bodied predatory fishes (Gorman 1988ab). Upland streams also exhibit longitudinal zonation in which habitat guilds of cyprinids change from headwater groups to midstream groups (Felley & Hill 1983).

Segregation and other distribution patterns may not be set in stone. Upland streams are generally considered to be stable habitats and distribution patterns of species assemblages may have been stable for thousands of years (Gorman 1987, 1988ab). Environmentally unstable systems, however, may prevent the formation of stable habitat guilds. In the South Canadian River, Oklahoma, microhabitat use and habitat breadth of four cyprinids was dynamic, changing with environmental conditions (Matthews & Hill 1980).

Presence of predators may also affect spatial distribution. Intensity of response is typically proportional to actual risk. In the presence of a relatively ineffective predator, Brassy Minnows, *Hybognathus hankinsoni*, did not seek as much shelter as they did when in the presence of a more effective predator such as Smallmouth Bass (*Micropterus dolomieui*) (Schlosser 1988a). Central Stonerollers, *Campostoma anomalum* (Fig. 12.56c), increased time spent in riffle habitat if pools contained predators (Schaefer 2001). Predation pressure can decrease available habitat and potentially increase competition (Gorman 1988b). Cyprinids typically follow the bigger fish–deeper habitat pattern of distribution that is thought to be the result largely of predator avoidance (Harvey & Stewart 1991). The explanation for such a distribution is simple: larger fish have a high risk of predation in shallow waters from birds and mammals (herons, raccoons, etc.). As the fish moves to deeper water, this predation risk decreases. For a small fish, however, the risk of mammalian or avian predation remains low, regardless of depth. Risk of predation from large fish is high for small prey fish—a reason for small fish to keep to the shallows. Larger fish are less likely to fall victim to piscivory, hence they are at a smaller risk in deeper water. This results in shallow water being the safest place for small fishes and deeper water being the safest habitat for larger fishes. Given that most cyprinids are small, different size classes of Hornyhead Chubs, *Nocomis micropogon*, unsurprisingly remained in refugia in the presence of predators (Schlosser 1988b).

Most cyprinids have high dispersal ability—some recolonize streams that dessicate completely, even within one year (Adams & Warren 2005). Young Bluntnose Minnows, *Pimephales notatus*, and Striped Shiners, *Luxilus chrysocephalus*, show strong dispersal capability into upstream environments (Schlosser 1987). Dispersal through riffles is affected by current velocity, riffle length, and threat of predation (Lonzarich et al. 2000; Schaefer 2001). Increasing velocity decreases movement across riffles (Schaefer 2001). Areas of high velocity, including artificial structures such as culverts, may completely block upstream movements (Warren & Pardew 1998). Dispersion of Rosyside Dace, *Clinostomus funduloides*, is not always associated with available habitat but with the presence of eddies or depositional areas, particularly in times of high flow. This may be a function of energetics or food availability (Freeman & Grossman 1993). Cyprinids can recolonize pools from neighboring pools within a month, and large-bodied individuals typically recolonize fastest (Lonzarich et al. 1998). In large-bodied cyprinids, such as the Colorado Pikeminnow, *Ptychocheilus lucius*, adults can move nearly 100 km/yr; such movements are typically upriver where temperature and food availability are favorable (Osmundson et al. 1998).

Movement of cyprinids within streams on short time scales is species dependent. In a study of the Blue Shiner, *Cyprinella caerulea*, most individuals remained in habitat patches although a small percentage moved between patches. The average movement was 131 m and the greatest movement was 332 m (Johnston 2000b), which differs significantly from observations of the Bluehead Chub, *Nocomis leptocephalus*, which can move >1,000 m (Albanese et al. 2003).

The Sacramento Pikeminnow, *Ptychocheilus grandis*, can move ≤550 m at night, typically returning to the same spot by daybreak (Harvey & Nakamoto 1999). Much of the difference in daily dispersal ability is likely associated with body size, though other environmental factors likely play a role as well. In general, elevated local abundances bolster colonization rates, which are typically greatest in large stream localities; high variability in flow regime can increase the risk of local extinction (Taylor & Warren 2001). Interestingly, high flow velocity at culvert road crossings is negatively correlated with minnow movement, and these types of crossings appear to greatly impede movement (Warren & Pardew 1998). Future studies of flow regime microhabitats in stream environments could be fruitful in determining distribution and dispersal potential of cyprinids.

Trophic Ecology

North American cyprinids feed on a wide range of food types and the group includes detritivores, algivores, planktivores, insectivores, and piscivores. Trophic specializations are reflected in the morphology of the jaws, pharynx, and gut, and this morphology is often used to infer diet (see morphology section). Gut content studies provide a more direct assessment of diet, but even these may not provide an accurate picture of the contribution of ingested items to growth (Evans-White et al. 2001). The fact that "unintended" food items (i.e., algae and detritis ingested while feeding on a benthic invertebrate) can be consumed along with intended prey items makes determination of functional trophic ecology difficult. Most cyprinids are probably facultative omnivores, capable of switching prey depending on availability and abundance (Williams & Williams 1980; Grimm 1988; Evans-White et al. 2001). In desert streams of the southwestern United States, e.g., floods greatly reduce the aquatic invertebrate community but do wash in large numbers of terrestrial insects. The diet of Spikedace, *Meda fulgida*, follows the availability of terrestrial insect food (Barber & Minckley 1983). Similarly, during brief inundations of the floodplain in a blackwater stream in Mississippi, Cherryfin Shiners, *Lythrurus roseipinnis*, moved out of the channel onto the floodplain and exploited terrestrial invertebrates and aquatic invertebrates associated with floodplain pools. While on the floodplain, the shiners actually ate more food and consumed a significantly different diet than did Cherryfin Shiners in the stream, primarily because of consumption of large numbers of terrestrial springtails (Collembola) (O'Connell 2003). Stable isotope data indicated that Central Stonerollers, *Campostoma anomalum*, traditionally believed to be herbivores, also fed on and assimilated grazer and collector invertebrates as well as filamentous green algae (Evans-White et al. 2001). Gut content studies of this species indicated that they consumed more diatoms than green algae (Burkhead 1980; Fowler & Taber 1985). Evans-White et al. (2001) speculated that Central Stonerollers either assimilate nutrients from diatoms and periphyton not detectable in stable isotopes, or that detritus and diatoms may be important for maintenance but not growth.

Though food availability clearly structures what animals can potentially feed on, inter- and intraspecific competition can determine what foods are actually consumed. Fathead Minnows, *Pimephales promelas*, e.g., show temporal segregation of resources between adults and juveniles. Nocturnal feeding occurs in adults and diurnal feeding in juveniles (Price et al. 1991). Later in the summer when the numbers of males declined, probably due to spawning mortality, the diet and foraging times of females and juveniles converged (Price at al. 1991). Even when food availability is unpredictable, cyprinids show resilience; e.g., larval Colorado Pikeminnows, *Ptychocheilus lucius*, grow optimally at high food densities but are resistant to starvation for ≤17.5 days after hatching (Bestgen 1996).

Ecosystem Function

Cyprinids form a huge proportion of ecosystem biomass and provide an important link in most ecosystems where they occur, either based on what they eat or what eats them. As mentioned above, minnows can eat almost any plant or animal that occurs in North American lakes and rivers. In this section, we discuss a few exemplary roles of minnow species functioning as consumers in ecosystems—either of plant material, invertebrates, or other vertebrates—and the effects those interactions have on ecosystem structure and function. We conclude our discussion of ecosystem function with a review of the cyprinid role in nutrient cycling.

Fishes in the genus *Campostoma* (Fig. 12.56c), the stonerollers, strongly influence stream ecosystems. *Campostoma* are grazers that specialize on algae (but see trophic ecology subsection and Evans-White et al. 2001). These fishes have a ridge on the lower jaw that functions as a scraper (Fig. 12.65). Stonerollers have a dramatic and pervasive impact on the distribution and standing crop of algae in streams (Matthews & Heins 1987). Extensive grazing of algae has an effect on other grazers in stream systems. Snails grow larger and delay reproduction in the presence of *Campostoma*, but crayfish are affected negatively, gaining less weight and exhibiting lower production (Vaughn et al. 1993). Exclusion experiments with *Campostoma* demonstrated that their grazing habits resulted in a decrease in algal standing crop and coverage by filamentous green algae, lower bacterial densities, and a decrease in benthic particulate organic matter. They stimulate an increase in primary productivity, blue-green algae, and invertebrate density (Gelwick & Matthews 1992). These changes occur rapidly and are observable for some time after *Campostoma* removal. Thus, schools of stonerollers, moving from one stream reach to another, could potentially modify the structural and functional characteristics of an entire stream (Gelwick & Matthews 1992). The impact of *Campostoma* may be affected by predators, particularly Largemouth Bass (*Micropterus salmoides*) that interact strongly with *Campostoma* to influence algal standing crop (Power et al. 1985). In small streams, Largemouth Bass and *Campostoma* rarely co-occur in pools. When present together, the bass generally are located in deep water and the *Campostoma* in shallow water (Power et al. 1985; Schaefer 2001).

Fathead Minnows, *Pimephales promelas*, can have substantial impact on the ecology of prairie potholes, affecting the invertebrate community, water clarity, and nutrient pools. Populations of the Fathead Minnow increase rapidly after invasion of new habitats and dramatically alter the composition, reduce the standing-crop biomass, and reduce production of the invertebrate community (Hanson & Riggs 1995; Zimmer et al. 2001b). Their populations can be large enough so that consumption rates of Fathead Minnows can equal invertebrate production (Duffy 1998). Such strong effects can restrict abundance of other insectivores. Nesting ducks and ducklings are largely insectivorous, and their abundance may be negatively correlated with presence of Fathead Minnows (Hanson & Riggs 1995). In wetlands with low abundance of macrophytes, dense populations of Fathead Minnows resulted in turbid conditions. When the species was present, the major phosphorus and nitrogen pools were phytoplankton, seston, macrophytes, and fishes. In the absence of Fathead Minnows, macrophytes, epiphyton, and aquatic invertebrates were the largest pools (Zimmer et al. 2001a).

Filter-feeding Sacramento Blackfish, *Orthodon microlepidotus*, selectively feed on zooplankton and large phytoplankton, resulting in an increase in nanoplankton. These fish effect a substantial increase in primary production and may affect secondary production in the lakes and reservoirs they inhabit (Byers & Vinyard 1990). These effects are similar to those in other filter-feeding fishes.

The Sacramento Pikeminnow, *Ptychocheilus grandis*, can serve as a significant predator, altering fish distribution when introduced (White & Harvey 2001). Their presence or absence changes the density of their prey species, Sculpins (*Cottus* spp.). Interestingly, since this is an intraspecific predator, young Sacramento Pikeminnows will also change their distribution depending on the presence or absence of adults (Gard 2005).

Cyprinids appear to function in storage and transport of nutrients in streams and lakes. In stream systems, fishes can represent a significant proportion (3–6%) of total nitrogen, and nitrogen excreted by fishes may represent 5–10% of total nitrogen uptake by algae (Grimm 1988). Studies of carbon, nitrogen, and phosphorus stoichiometry in Canadian lakes indicated that the included cyprinids (Fathead Minnow, *Pimephales promelas*, Northern Redbelly Dace, *Chrosomus eos*, Finescale Dace, *C. neogaeus*, and Pearl Dace, *Margariscus margarita*) were lower in phosphorus than other fishes (Sterner & George 2000). Cyprinids concentrate these nutrients from their diet—levels in the gut contents are lower than that in the body tissues. Isotopic signatures indicate that the majority of cyprinid carbon is derived from planktonic production, rather than from terrestrial or benthic sources. Benthic primary productivity is associated with fish density; this could indicate that minnows in the water column function as nutrient transporters of terrestrial nutrients to benthic pools (Gido & Matthews 2001).

Parasites

Many parasites use cyprinid fishes as hosts. For example, one relatively well-studied species, the Golden Shiner, *Notemigonus crysoleucas*, is host to ≥68 species of parasites, including fungi, protozoans, mongeneans, trematodes, cestodes, nematodes, acanthocephalans, hirudineans, and crustaceans (Hoffman 1999) as well as ≥8 species of freshwater bivalves (OSUDM 2010). Parasites may use cyprinids as either intermediate or definitive hosts, depending on the species (synopses by Margolis & Arthur 1979; Hoffman 1999). Of cyprinid parasites, unionid bivalves (freshwater mussels), flatworms (trematodes and cestodes), and myxozoans are the most widely studied. Here, we review the diversity and basic life history of cyprinid parasites. We follow this with descriptions of modes of parasitism, host specificity, and infestation/population dynamics and conclude with our basic understanding of how parasitism affects the morphology of minnows.

Bivalves are well known as parasites on North American freshwater fishes. The larvae of unionid bivalves attach to the fins or gills of fishes for a brief period. The parasitic stage generally lasts for 2–4 weeks, at which point the glochidia metamorphose, are shed from the gills, and drop to the substrate, where they develop into adults. Some bivalves exhibit host specificity, but others are generalists, infesting a wide and diverse range of taxa. Several major avenues exist for transferring glochidia from the gravid female bivalves to the gills of the host fish. *Strophitus subvexus*, e.g., releases glochidia bound in a copious mucosal medium that apparently entangles fishes indiscriminately (Haag & Warren 1997). Others, such as *Pleurobema furvum*, release glochidia in packages called conglutinates (Fig. 12.83) that drift passively with the stream current. These packets are eaten by minnows and subsequently burst at which point the developing glochidia attach to the gills of the host. Specificity of mussels and their glochidia for host fishes varies from species to species. For example, *S. subvexus* are capable of parasitizing

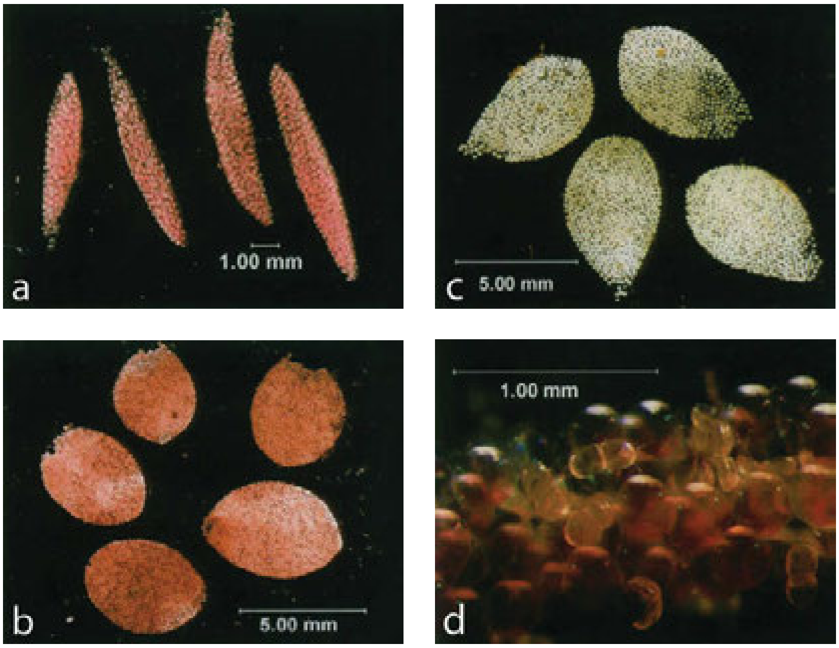


Figure 12.83. Freshwater mussel glochidial (larval) packets. (a) Conglutinate packets of developing glochidia of *Fusconaia cerina*, which uses a variety of stream cyprinids as host fishes. (b and c) Conglutinate packets from two *Pleurobema decisum* females, another species using cyprinids as hosts, from the same population (Buttahatchee River, Monroe County, Mississippi) demonstrating intrapopulation color variation. (d) Conglutinate with mature glochidia (light orange) and undeveloped eggs (dark orange). Note the large proportion of undeveloped eggs and the similarity between the mature glochidia and adult bivalves (from Haag & Warren 2006; photograph by W. R. Haag).

Suckers (Catostomidae), darters (Percidae, Perches) and several species of minnows. *Pleurobema furvum*, in contrast, metamorphoses almost exclusively on cyprinids, developing on the Largescale Stoneroller, *Campostoma oligolepis*, Alabama Shiner, *Cyprinella callista*, Blacktail Shiner, *C. venusta*, and Creek Chub, *Semotilus atromaculatus* (Haag & Warren 1997). Our perception of host specificity in North American fish parasites may be a function of our understanding of species-level diversity of these organisms.

Myxozoans are also parasites of North American minnows. These organisms have two alternate hosts. Different species parasitize different tissues and species, but they generally parasitize an oligochaete worm and a minnow as alternating hosts. Spores of *Myxobolus pendula* develop within cysts on the gill arch of the Creek Chub, *Semotilus atromaculatus*, among other minnow species (Koehler et al. 2004). These spores cause a reaction of the gill tissue, creating a capsule around the cysts. This capsule protects the host but does not seem to inhibit diffusion of oxygen or nutrients to the developing spores. Multiple species of myxozoan can coexist within one individual (e.g., ≤4 species simultaneously parasitized Spottail Shiners, *Hudsonius hudsonius*, in the St. Lawrence River, Quebec); two occurred within striated muscle tissue, one within loose connective tissue, and one in the brain (Marcogliese & Cone 2001).

The first life stage of most trematodes is a free-swimming stage, the miracidium, that infests pond snails (*Physa gyrina*). Miracidia transform into cercariae, and emerge from the snail in 25–28 days as metacercaria. The metacercarial stage encysts in the tissues of the next host, which can be a cyprinid, where it further develops (Goater et al. 2005). One trematode, *Ornithodiplostomum ptychocheilus*, encysts in the optic theca of minnows, but another, *Posthodiplostomum minimum*, infects the mesenteries. If the infected minnow is eaten by piscivorous birds, immature trematodes emerge from the metacercarial cyst and develop in the avian gut where they mature and reproduce. Eggs are released and disseminated into the environment via fecal matter. Natural intensities of *Ornithodiplostomum ptychocheilus* infestations of the Fathead Minnow, *Pimephales promelas*, range from 5–123 metacercariae/host, and parasites have survived a laboratory-simulated winter (Sandland et al. 2001). Another trematode, *Allocreadium wallin*, is an intestinal fluke in the host Creek Chub, *Semotilus atromaculatus* (Willis 2001). This parasite's first intermediate host is a sphaeriid clam (*Pisidium* spp.). The second intermediate host for this species is an amphipod, and *A. wallin* reaches sexual maturity in minnows. Intensity and abundance increases are correlated with increasing host size. Species of *Dactylogyrus* (Trematoda), commonly referred to as gill flukes, are typically specific to a single species or closely related species of cyprinid (Mizelle & McDougal 1970; Cloutman & Rogers 2005). Speciation in this genus is likely the result of co-evolution (Cloutman & Rogers 2005).

Population dynamics of parasites can change with alterations to the ecological state of a stream. Longnose Dace, *Rhinichthys cataractae*, inhabiting more productive and thus more eutrophic environments, had greater infestations of trematode metacercaria (genus *Neascus*) (Vinikour 1977). Spottail Shiners, *Hudsonius hudsonius*, had a higher incidence of infection by myxozoans in habitats with higher oligochaete populations; oligochaetes served as an intermediate host for the myxozoans (Cone et al. 2004). Higher infection rates occurred in areas where anthropogenic organic enrichment resulted in eutrophication (Marcogliese & Cone 2001). Enrichment causes increased numbers of oligochaetes that could drive greater infection rates.

We do not currently have a solid understanding of the ecological impact of parasitism on the family Cyprinidae. Though many species harbor bivalve parasites and survive following the infestation, infestation effects on fitness, metabolism, or any other ecological parameter are not understood. Future studies of metabolic, physiological, and behavioral effects of parasitism will be necessary to deepen our understanding of parasite ecology. We do have a basic understanding that parasitism can alter the morphologies of their cyprinid hosts. In the Fathead Minnow, *Pimephales promelas*, crania grew deeper and wider in individuals from areas infected with the brain-encysting *Ornithodiplostomum ptychocheilus* relative to individuals from an adjacent, uninfected area (Sandland & Goater 2000). This infestation also caused decreased activity levels (Shirakashi & Goater 2002), and behavioral changes are most evident early in infestation—well-developed infestations seem to alter behavior less significantly (Shirakashi & Goater 2005). Vertebral deformities are caused by trematodes of the genus *Apophallus* in the Northern Pikeminnow, *Ptychocheilus oregonensis*, and Chiselmouth, *Acrocheilus alutaceous* (Cunningham et al. 2005).

CONSERVATION

An estimated 46% of the native North American cyprinid fauna is imperiled: 49 species are considered Vulnerable, 20 species Threatened, 47 species Endangered, and 11 species Extinct (Jelks et al. 2008). Most species are affected by anthropogenic impacts on habitat, including the erection of dams, agricultural practices, industrial pollution, and interactions with invasive species. Some imperiled cyprinids are naturally rare and thus are particularly susceptible to environmental fluctuations and anthropogenic pressures. Although any one of these factors can cause extirpation of a population by itself, a sustained combination of these factors generally results in the decline of a species (Moyle & Leidy 1992). Here we present specific examples of anthropogenic impacts on native North American cyprinds. This is not an exhaustive list, but the majority of imperiled cyprinids are facing at least one of these issues, and most are facing several threats. Thus, a multipronged approach will be necessary to any conservation plan. The conservation status of Vulnerable, Threatened, or Endangered cyprinids discussed here is based on Jelks et al. (2008) and placed in parentheses after the name of the species.

Dams and Flow Modification

Dams have a profound impact on riverine habitat, altering flow regime, blocking migration and other movements, and impacting water quality (Baxter 1977; Winston et al. 1991; Bonner & Wilde 2000). Many cyprinid species in large rivers and prairie streams are members of a reproductive guild that relies on flood events for successful spawning; members of this guild are broadcast spawners with non-adhesive, semi-buoyant eggs. For these species, quick flows are crucial in the first 10–30 min after fertilization for the perivitelline space to fill with water. Once this occurs, the semi-buoyant eggs can be maintained in the water column with minimal flow. If the eggs settle to the bottom, they will be covered in silt and will cease development. The dependence of these fishes on fast flows during spawning renders them particularly susceptible to structures, such as dams, that decrease or moderate flow rates (Platania & Altenbach 1998; Bonner & Wilde 2000). The Rio Grande Silvery Minnow, *Hybognathus amarus* (Endangered), Rio Grande Shiner, *Notropis jemezanus* (Endangered), and Pecos Bluntnose Shiner, "*N.*" *simus pecosensis* (Endangered) have been extirpated from an 89 km reach of the upper Pecos River, New Mexico–Texas, after dam construction (Platania & Altenbach 1998). Rio Grande Silvery Minnows persist in the middle Rio Grande, spawning when the water velocity is at its maximum, but a number of other members of the semi-buoyant egg reproductive guild have been extirpated from this system (Platania & Atlenbach 1998). In the Canadian River, Oklahoma, variation in mean annual discharge has decreased substantially following the construction of four dams between 1938 and 1967. Populations of the Plains Minnow, *Hybognathus placitus* (Vulnerable), Peppered Chub, *Macrhybopsis tetranema* (Endangered), Arkansas

River Shiner, *Notropis girardi* (Endangered), and Flathead Chub, *Platygobio gracilis* (no status), have decreased dramatically, particularly in lower reaches of the river where discharge and stream morphology were most affected (Bonner & Wilde 2000).

In the Sacramento River system, California, Splittails, *Pogonichthys macrolepidotus* (Vulnerable; Fig. 12.48), rely on inundation of the flood plain for spawning, rearing, and foraging habitat. Good young-of-the-year production occurs only in years of flooding (Sommer et al. 1997). Splittails inhabit the San Joaquin estuary as adults and migrate up the Sacramento River in winter and spring where they spawn on flooded vegetation (Meng & Moyle 1995). Due to large variations in flooding from year to year, the population size exhibits significant annual fluctuations as does the year-class strength (Daniels & Moyle 1983). Year-class strength is correlated with total annual flow of the Sacramento River (Daniels & Moyle 1983), and increased control of flooding has hindered reproduction of these fish. Riverine flow likely is essential to not only transport larval Splittails to the estuary but also to maintain suitable levels and positions of freshwater-saltwater mixing zones (Meng & Moyle 1995). The adults feed in brackish water, and the Splittail is one of few cyprinid species capable of tolerating these conditions (see physiology section). Stocking of these fish is ineffective as a conservation measure; the stock-recruitment relationship is fairly weak with stocking effort explaining <25% of the year-to-year population variability (Meng & Moyle 1995). Splittails have high annual egg production and a relatively long lifespan; thus, these fish can persist despite drought years when recruitment can be nearly nonexistent (Daniels & Moyle 1983; Sommer et al. 1997). The highly restricted range and unique attributes of these fish warrant careful attention and protection to ensure their persistence.

The construction of dams in the Colorado River had catastrophic effects on the endemic cyprinid fauna (Minckley 1991b). Cold water released from the hypolimnion of reservoirs, the fragmenting of habitat by the dams, the impact of dams on stream morphology, the altered seasonal flow regimes, and effects of non-native fishes stocked in reservoirs have all had profound effects. The Humpback Chub, *Gila cypha* (Endangered; Fig. 12.56e), and Bonytail Chub, *G. elegans* (Endangered), both occurring in the Colorado River, historically maintained long-term effective population sizes of 48,800 and 44,800, respectively (Garrigan et al. 2002). These population numbers are staggering compared with about 2,000 Humpback Chubs and roughly 100 Bonytail Chubs estimated to currently persist in the wild. As a result primarily of the effects of dams, millions of dollars have been spent and continue to be spent on hatcheries, surveys, and other recovery actions for these fishes (Minckley et al. 2003).

Flood events can restructure the stream bed, creating gravel bars and backwater habitat. These environments provide critical rearing habitat for larval and juvenile cyprinids. In the Colorado River system, lack of appropriate backwater habitat is implicated in the low recruitment of the endangered cyprinids of that system. Flood control combined with the constant reservoir release for electricity production has been accompanied by degradation of gravel bars and backwater habitat. Recently, the Army Corps of Engineers has been releasing water from reservoirs in an attempt to mimic flood conditions in the Colorado River. These artificial floods have created gravel bars and backwater habitat (Poff et al. 1997) but it is not clear that artificial floods increased survival of larval and juvenile native cyprinids, although the floods did reduce the numbers of invasive introduced fishes (Valdez et al. 2001). Similarly, the absence of appropriate spawning and larval habitat has had a profound effect on the Bonytail Chub, *Gila elegans* (Endangered). Adult fish can survive in reservoir habitats, but little or no successful spawning and recruitment has occurred since the river was impounded. Adult Bonytail Chubs are long-lived (>40 years) and persisted in reservoirs until the 1980s when captive breeding efforts were started (see genetics section). These fish are now successfully raised in the U.S. Fish and Wildlife Service Dexter Fish Hatchery, and juveniles are being released into the wild. The survival of the Bonytail Chub depends on continued release of hatchery-raised juveniles perhaps in perpetuity.

Dams and their impoundments have a profound impact on turbidity (see physiology and ecology sections). The decrease in flow in large reservoirs results in a loss of sediment from the water column (Pflieger & Grace 1987; Hesse et al. 1989). Although the change from turbid to clear may be viewed as an improvement of water quality, clear water can be detrimental to native fishes adapted to turbid conditions. The Missouri River drainage is an excellent example of the impact that changes in water clarity can have on native cyprinids. Historically, the Missouri River and its major tributaries were characterized by high amounts of suspended sediments, and the sediment load of the Missouri River markedly increased the turbidity of the Mississippi River downstream of their junction. Following dam construction in the system, decreases in turbidity along with other changes to the habitat allowed piscivorous species, many of which are sight feeders, to thrive. The presence of piscivores in Missouri River tributaries is correlated with the absence of turbid river cyprinids such as the Western Silvery Minnow, *Hybognathus argyritis* (Vulnerable), Plains Minnow, *H. placitus* (Vulnerable), Sturgeon Chub, *Macrhybopsis gelida* (Vulnerable), and Flathead Chub, *Platygobio gracilis* (no status) even when the habitat otherwise appears to be suitable (Quist et al. 2009).

Dams and their impoundments fragment habitat and affect populations both upstream and downstream. After the creation of the Altus Dam in 1946 on the North Fork Red River, Oklahoma, four minnow species were extirpated upstream of the dam (Winston et al. 1991). Extensive sampling of the North and Salt forks revealed that the cyprinid species Prairie Chub, *Macrohybopsis australis* (Vulnerable), Red River Shiner, *Alburnops bairdi* (no status), Chub Shiner, *A. potteri* (no status), and Plains Minnow, *Hybognathus placitus* (Vulnerable), which were historically common in the Red River, were either absent or rare in the North Fork upstream of the Altus Dam (Winston et al. 1991). Several non-mutually exclusive factors could have led to the extirpation of these fishes. First, the reservoir above the dam created habitat for piscivorous fishes that may have preyed heavily on these cyprinids. Second, the semi-buoyant eggs of these cyprinids may have been washed into the reservoir, where an inhospitable environment halted their development. Third, the dam blocked new colonizers from moving upstream to reinhabit the area after drought or floods caused local extirpation (Winston et al. 1991).

Dams also can interfere with potadromous migrations of cyprinids, such as that of the Colorado Pikeminnow, *Ptychocheilus lucius* (Endangered) (Fig. 12.84; Rinne & Minckley 1991). Colorado Pikeminnows undergo long (>150 km), migrations to use prime spawning and feeding habitats. These fish evolved during periods of episodic fluctuations in river levels and are quite capable of surviving under these conditions (Tyus 1986). Most authors agree that construction of dams in the 1960s was the proximate cause of decline of this species. The main detrimental effects of these dams include flowing water habitat loss due to reservoirs, cold flows downstream of dams decreasing suitable habitat and reproductive success, and loss of backwater habitat (due to lack of spring flows and fluctuations) that is used extensively by young individuals (Holden & Wick 1982). A low growth rate coupled with lowered temperature (as a result of dam construction) are likely other key reasons for the decline of these fish (Kaeding & Osmundson 1988).

Interestingly, floodplain isolation seems to have served to protect the surviving populations of the Oregon Chub, *Oregonichthys crameri* (Endangered), which is endemic to the Willamette Valley, Oregon. This minnow was once distributed throughout that valley; however, the Oregon Chub now inhabits <2% of its historic range (Bond & Long 1984), which led to federal listing as Endangered in 1993. In an investigation of this minnow, the largest populations occurred in habitats isolated from the flood plain, where connectivity was low (Scheerer 2002). These areas also were less likely to contain non-native fish species than areas of high connectivity. Oregon Chubs were either absent or present only in small numbers when non-native fishes were present. These data suggest that the isolation of these fish from non-native fishes (as a result of lower connectivity) actually protects them from the threats that non-native fishes would pose (Scheerer 2002).

Agriculture and Development

Habitat modifications, increased turbidity, nutrient runoff, and other pollutants associated with agriculture and development present another major threat to cyprinid fishes. The Thicktail Chub, *Gila crassicauda* (Extinct), was present in the Pajaro and Salinas Rivers, California (Gobalet & Jones 1995), as well as in the Napa and Coyote River drainages (Gobalet et al. 2004). Thicktail Chubs likely were present throughout the Central Valley of California in lowland areas, in Clear Lake, and in tributaries to San Francisco Bay (Moyle 2002). The Thicktail Chub represented the third most abundant fish in a central California Native American midden, which dated from roughly 1,000 to 200 years before present (Schultz & Simons 1973). The last known Thicktail Chub was captured in 1958, and subsequent, intensive sampling across its putative range was unsuccessful in finding any additional individuals (Moyle 2002). Extinction of the Thicktail Chub likely is due to its inability to adapt to modification of the habitat, land reclamation, and introduction of non-native predators and competitors.

Agricultural practices, particularly overgrazing, can result in increased sedimentation and turbidity in streams (see physiology and ecology sections). Spawning events and number of eggs produced by the Tricolor Shiner, *Cyprinella trichroistia*, a crevice-spawning cyprinid, declined with increased levels of suspended sediment. This

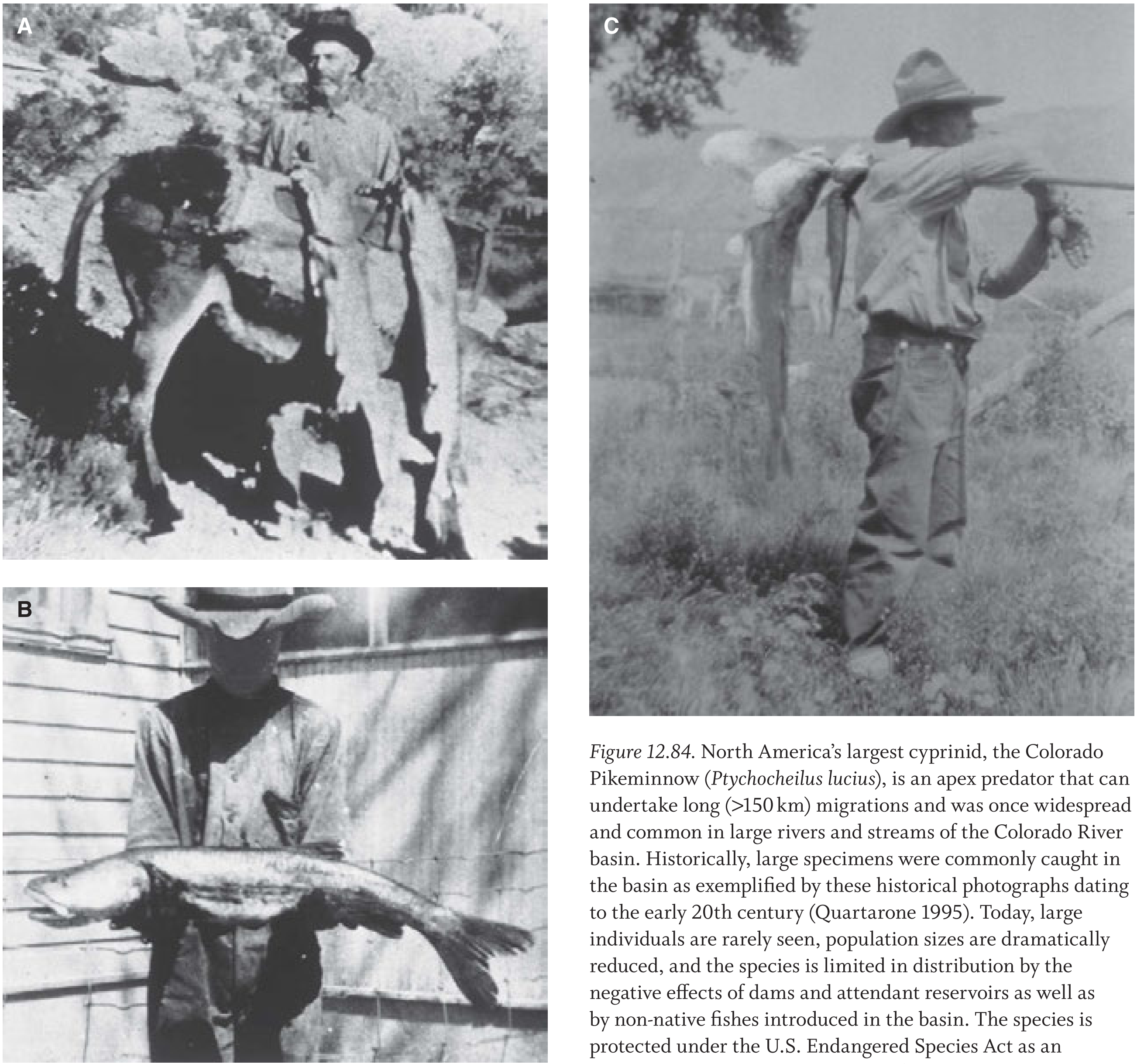


Figure 12.84. North America's largest cyprinid, the Colorado Pikeminnow (*Ptychocheilus lucius*), is an apex predator that can undertake long (>150 km) migrations and was once widespread and common in large rivers and streams of the Colorado River basin. Historically, large specimens were commonly caught in the basin as exemplified by these historical photographs dating to the early 20th century (Quartarone 1995). Today, large individuals are rarely seen, population sizes are dramatically reduced, and the species is limited in distribution by the negative effects of dams and attendant reservoirs as well as by non-native fishes introduced in the basin. The species is protected under the U.S. Endangered Species Act as an endangered species and extensive efforts are underway to prevent extinction of this unique fish. (A) Two large Colorado Pikeminnow hang off a burro. (B) Colorado Pikeminnow caught near Jensen, Utah (Green River drainage), in the 1930s. (C) A farmer carries two Colorado Pikeminnows caught as he irrigated a hayfield in about 1934 (photographs courtesy of the Upper Colorado River Endangered Fish Recovery Program, U.S. Fish and Wildlife Service, Denver, Colorado).

species also delayed spawning at higher levels of suspended sediment until these levels declined, underscoring the importance of visual cues during reproduction (Burkhead & Jelks 2001). Increased turbidity has been implicated in the decline of other cyprinids, including the Proserpine Shiner, *Cyprinella proserpina* (Endangered) (Hubbs & Echelle 1972), and Bridle Shiner, "*Notropis*" *bifrenatus* (Vulnerable) (Sabo 2000).

The effects of industrial pollutants in the environment are well publicized and industrial spills are responsible for the extirpation of fishes from several stream reaches. Chemical spills in the upper Tennessee River system may be responsible for loss of some cyprinids. For example, the Slender Chub, *Erimystax cahni* (Endangered), historically occurred in the Holston, Clinch, and Powell Rivers in Tennessee. Populations in both the Holston and Powell Rivers now are extirpated, probably as a result of industrial pollution (Jenkins & Burkhead 1994). The Turquoise Shiner, *Erimonax monachus* (Threatened; Fig. 12.56a), is another endemic of the Tennessee River drainage. This species disappeared from most of its range; however, the population in the North Fork Holston River is rebounding, presumably as a result of pollution abatement in Saltville, Virginia, where previous pollution had lowered its abundance (Jenkins & Burkhead 1994; Fig. 12.21). The Blue Shiner, *Cyprinella caerulea* (Endangered), was historically endemic to the Cahaba and Coosa River systems within the Mobile Basin (Boschung & Mayden 2004). Currently, six extant isolated populations remain in the upper Coosa River in northeast Alabama, northwest Georgia, and southeast Tennessee. The Cahaba River populations are no longer extant. Extirpation from the Cahaba River occurred as nitrification increased from high sewage loads (Stephens & Mayden 1999).

Sediments also can harbor chemical pollutants that may impact cyprinids. Lake Pinchi, a large lake (>5,300 ha) in northern British Columbia, was mined for mercury from 1940 to 1944, and the fishes of that region continue to exhibit effects of contamination. Northern Pikeminnows, *Ptychocheilus oregonensis*, have methyl-mercury concentrations about 2–4 times higher than Northern Pikeminnows from similar, but unpolluted, nearby lakes and higher methyl-mercury concentrations than similar size, sympatric Rainbow Trout (*Oncorhynchus mykiss*). Body size and methyl-mercury concentration are correlated in the Northern Pikeminnow but not in the Rainbow Trout. This is attributed to the higher trophic position and slower growth rate of the Northern Pikeminnow, resulting in biomagnification of the mercury (Weech et al. 2004). Rapid biomass accumulation in the Rainbow Trout results in tissue mercury concentrations similar to that of prey items, but Northern Pikeminnows do not convert prey biomass as efficiently, resulting in heightened levels of methyl-mercury (Weech et al. 2004).

Non-Native Species

The introduction of non-native species has profound, usually negative, effects on native species. Introduced predators can have severe and long-lasting impacts on native fauna. Cyprinids are no exception. This can be particularly acute if the native taxon is naive to an introduced predator. The Little Colorado Spinedace, *Lepidomeda vittata* (Threatened), occurs in disjunct populations in northern Arizona and is extant in only three counties where it occupies a wide variety of habitats. The abundance and range of these fish has diminished since the introduction of Rainbow Trout in the mid-1800s (Blinn et al. 1993). Experiments demonstrated high Rainbow Trout predation on the Little Colorado Spinedace, which exhibited almost no predator avoidance (Blinn et al. 1993). The introductions of Rainbow Trout may be partly responsible for the scattered, relatively small distribution of the Little Colorado Spinedace.

Centrarchid invasives also have detrimental effects on native fish populations. In the Umpqua River system in the Pacific Northwest, the Smallmouth Bass (*Micropterus dolomieui*) is implicated in the decline of the Umpqua Chub, *Oregonichthys kalawatseti* (Vulnerable). Smallmouth Bass were stocked in Oregon in 1924 and 1925 (Simon & Markle 1999) but did not gain access to the Umpqua River system until 1964 during a flooding event, after which they became distributed across the Umpqua River basin by the late 1970s. This was followed by a substantial decline in the Umpqua Chub, which by 1998 disappeared from 50% of the sites it previously occupied, while Smallmouth Bass abundance increased at all spots from which Umpqua Chubs were extirpated. Other species in the system, such as the Umpqua Pikeminnow, *Ptychocheilus umpquae*, disappeared from 13% of formerly occupied sites (Simon & Markle 1999).

Introduced predators such as the Northern Pike (*Esox lucius*), Largemouth Bass (*Micropterus salmoides*), and Smallmouth Bass can have a dramatic influence on species richness, reducing the species richness of native cyprinids by as much as two-thirds, compared with similar, predator-free lakes (Findlay et al. 2000). Introduced sight-feeding predators have also been implicated in the disappearance or reduction in numbers of native cyprinids in rivers (see previous two paragraphs).

Introduced North American species may also compete with native cyprinids. Red Shiners, *Cyprinella lutrensis*, have been introduced into the Colorado River system (see diversity and distribution section) as forage for gamefishes and has become widespread. In the Gila River, a tributary to the Colorado River, Red Shiners overlap in range with Spikedace, *Meda fulgida* (Endangered). The two cyprinids share similar spawning habitat and have general (though not exact) habitat overlap. Red Shiners are more tolerant of turbidity, high temperatures, and low dissolved oxygen. These factors make Red Shiners an effective competitor, especially against Spikedace, and may be influential in restricting its range (Rinne 1991).

Introduced parasites pose a threat to native cyprinids. The western cyprinids Roundtail Chub, *Gila robusta* (Vulnerable), and Woundfin, *Plagopterus argentissimus* (Endangered), e.g., are greatly affected by *Bothriocephalus acheilognathi*, an Asian tapeworm. Red Shiners, *Cyprinella* *lutrensis* (an invasive species in that area), may have carried *B. acheilognathi* from other parts of the country, where the tapeworm was originally introduced from Asia via Grass Carp, *Ctenopharyngodon idella* (Heckmann et al. 1986). *Bothriocephalus acheilognathi* generally has two hosts, a copepod and a cyprinid; the tapeworm can block the gastrointestinal tract, perforate the intestine, and destroy the internal mucosa. They generally concentrate in the anterior portion of the gastrointestinal tract. Dense infestations can result in reduced growth, deformities, suppressed swimming, and lowered reproduction. The number of tapeworms infesting an individual is negatively correlated with fish length and weight (Brouder 1999). This parasite is generally not alone when infesting fish species; in addition to the Asian fish tapeworm, six other parasite species occurred in specimens of Woundfin (Heckmann et al. 1986). *Bothriocephalus acheilognathi* occurred in every cyprinid sampled in Arizona and Nevada reaches of the Virgin River (Heckmann et al. 1993). Interestingly, despite the presence of infested host fishes in tributaries of the Colorado River, *B. acheilognathi* is unknown from hosts in the main stem of the river. This may be due to lower temperatures in the Colorado River compared with those of its tributaries because *B. acheilognathi* requires water temperatures >20°C (Brouder & Hoffnagle 1997).

Invasive species can also impact bioaccumulation of toxic substances as exemplified by the association of the non-native Overbite Clam, *Potamocorbula amurensis*, and the native Splittail, *Pogonichthys macrolepidotus* (Endangered). The Overbite Clam is an invasive species in the Sacramento River estuary, California. This species, introduced from Asia, has a substantially different physiology from that of native invertebrates. The Overbite Clam was first captured in the estuary in 1986 and currently accounts for more than 95% of the benthic invertebrate biomass in some areas (Carlton et al. 1990). This bivalve possesses a selenium loss rate constant an order of magnitude lower than that of other co-occurring invertebrates and is much higher in selenium concentration than other invertebrate food sources (Stewart et al. 2004; Linville et al. 2002). Although selenium is an essential nutrient, the difference between the nutritional and toxic concentrations is small and at high levels can be toxic to fishes (Hamilton 2004; see physiology section). Splittails feed extensively on these bivalves, particularly when numbers of their natural prey, mysid shrimp, decline, and high selenium concentrations could further endanger Splittail populations (Feyrer et al. 2003).

Naturally Small Populations

The Moapa Dace, *Gila coriacea* (Endangered), endemic to the upstream-most 4 km of the 40 km long Muddy River, Nevada (formerly the Moapa River), is a spring-dependent species and is protected as Endangered under the U.S. Endangered Species Act. This fish, although locally abundant, has an exceedingly limited range, making it vulnerable to local perturbations. These include a flash fire in 1994 that is believed to have reduced the population from about 500 to 34 individuals (Scoppettone et al. 1998); invasive species, including the Shortfin Molly (*Poecilia mexicana*) and Blue Tilapia (*Oreochromis aurea*) (Scoppettone 1993; Scoppettone et al. 1998); and groundwater pumping (Mayer and Congdon 2008).

The Desert Dace, *Eremichthys acros* (Threatened; Fig. 12.19), is also a spring-dwelling endemic, residing in several, isolated, hot springs in Soldier Meadow, Nevada (Vinyard 1996, 1997). These fish occur in waters much warmer than typical of cyprinids, ranging from 13 to 38°C. Alterations to habitat such as water withdrawals for agriculture significantly reduced abundance of this fish (Vinyard 1997). In addition, threats from introduced predators and competitors, such as the Largemouth Bass and Goldfish, *Carrasius auratus*, are of special concern to the conservation of the Desert Dace (Vinyard 1997). The small extent of habitat (and lowered total population numbers as a result) makes for an especially precarious position of these fish. Perturbations normally absorbable by higher population levels may have a significant impact on population processes in these situations.

The Borax Chub, *Siphateles boraxobius* (Endangered), another example of a range-restricted cyprinid, is endemic to the Alvord Basin, southeast Oregon and northwest Nevada, where it is restricted to Borax Lake and some tributaries. The small range of this fish is a primary concern, but other factors also contribute to its endangered status. The downstream reservoir of Borax Lake, termed Lower Borax Lake, previously sustained the Borax Chub, though reproduction was not confirmed (Williams & Bond 1983). In 1979, the outflow to Lower Borax Lake was diverted, and Borax Chubs are no longer found in the reservoir (Williams & Bond 1983), thus further restricting the habitat available to the species.

The Bluehead Shiner, *Pteronotropis hubbsi* (Vulnerable; Fig. 12.56f), inhabits lowland streams and swamps in Illinois, Arkansas, Texas, Oklahoma, and Louisiana. Though widely distributed, these fish are not abundant (except in spawning aggregations), and the few populations are isolated. The only population in Illinois occurred in Wolf Lake, about 443 km from the nearest known population in Arkansas. The Wolf Lake population was extirpated by chemical spills in 1974 and 1979 as a result of train derailments (Burr & Warren 1986a). This disjunct distribution suggests recent habitat alteration (e.g., channelization, dredging, sedimentation), bolstered by the fact that much of the Missouri and Arkansas lowlands were once covered by cypress swamps before settlement of these areas (Fletcher & Burr 1992).

COMMERCIAL IMPORTANCE

Commercial exploitation of North American cyprinids is largely limited to the bait industry. Though cyprinids are widely bought and sold in the aquarium industry, nearly all species in that trade are not native to North America. Though acknowledging the beauty, diversity, and lucrative nature of cyprinids in aquaria, we restrict discussion here to North American cyprinids used as baitfish or food.

Although several species of cyprinids are sold as bait, the Fathead Minnow, *Pimephales promelas*, and Golden Shiner, *Notemigonus crysoleucas*, are among the most widely sold and support a relatively extensive pond culture bait industry. In Arkansas alone, an estimated six billion bait minnows (mostly Golden Shiners and Fathead Minnows) are raised each year and shipped around the country (Stone et al. 2009). The relative ease of commercial pond culture, as well as the popularity and hardiness of these two minnow species, have led to their introduction across the United States well outside of their native range. The Fathead Minnow has been introduced in 24 states and the Golden Shiner in 21 states outside of its natural range (Boydstun et al. 1995). Other species commonly sold as bait include the Spottail Shiner, *Hudsonius hudsonius*, Sand Shiner, *Miniellus stramineus*, Hornyhead Chub, *Nocomis biguttatus*, Creek Chub, *Semotilus atromaculatus*, Finescale Dace, *Chrosomus neogaeus*, and Pearl Dace, *Margariscus margarita* (Meronek et al. 1997b). Estimates of the total value of baitfish sold in six states (Illinois, Michigan, Minnesota, Ohio, South Dakota, and Wisconsin) was >$145 million in 1992 (Meronek et al. 1997a). In 1998, the farm-gate value of baitfish production in Arkansas was estimated at $23 million with an economic impact of 6 to 7 times that amount (Stone et al. 2009). In Ontario, an annual baitfish business reached $12.4 million, which consisted of roughly 11 million dozen fish sold (OMNR 1986). This economic value is likely >$1 billion annually in Canada alone (Litvak & Mandrak 1993). Baitfishes, which are typically cyprinids, are used across North America, so the total commercial importance of North American cyprinids as baitfishes is likely much higher. Large-scale collection for bait has likely played a role in the decline of some species; of the species that are legally sold as baitfishes in Canada, 12 are listed as Vulnerable and 3 as Threatened (Campbell 1992).

The only North American cyprinid that is commercially important as a food fish is the Sacramento Blackfish, *Orthodon microlepidotus*. This species was described originally from specimens obtained from the San Francisco fish market (Ayres 1854). The Sacramento Blackfish is harvested from Clear Lake, San Luis reservoir, and Lahontan reservoir for sale in Asian markets in several California cities (Moyle 2002). In 1988, more than 363,800 kg of Sacramento Blackfish were harvested from the Lahontan reservoir (Sevon 1988). This species is considered a possible candidate for aquaculture because of its high production potential (Cech et al. 1979; Capagna & Cech 1981).

Mylocheilus caurinus was served historically as whitefish to customers of hotels in the Columbia River Basin, British Columbia (Jordan & Evermann 1902; McPhail & Lindsey 1970), and Eastern Silvery Minnows are reputed to be tasty when deep fried (Schwartz 1963). Tastes have changed, and sadly, the days when one could enjoy a hearty plate of minnows are long past.

LITERATURE GUIDE

Cyprinid Fishes by Winfield & Nelson (1991) provides an excellent overview and introduction to the biology and distribution of the family Cyprinidae. Several regional faunal guides contain excellent information on the biology, distribution, and identification of North American cyprinid fishes. Six of these stand out for the depth of the information they provide and the quality of their illustrations. *Freshwater Fishes of Canada* (Scott & Crossman 1973) provides detailed information, including biology, distribution, and parasitism of cyprinids in that country. *Fishes of Alabama* (Boschung & Mayden 2004) is notable for the outstanding illustrations by Joe Tomelleri. *The Fishes of Tennessee* (Etnier & Starnes 1993) contains excellent color photographs and a well-researched identification key. *Freshwater Fishes of Virginia* (Jenkins & Burkhead 1994) also contains excellent color photographs of some species, and much interesting information on natural history. Together, the latter three texts describe the biology of the majority of North America's cyprinid fauna. The biology and conservation status of many western cyprinids are reviewed by Moyle (2002) in *Inland Fishes of California* and McPhail (2007) in *The Freshwater Fishes of British Columbia*. *Freshwater Fishes of Mexico* (Miller et al. 2005) provides information on the distribution and identification of the Mexican cyprinid fauna.

G. R. Smith (1981) detailed the fossil record of North American fishes and contains a valuable list of references for any reader interested in the distribution and age of cyprinid fossils. Reviews of ecology, systematics, and behavior can be found in Matthews & Heins (1987), Matthews (1998), and Mayden (1992).

Acknowledgments

We thank Elizabeth Johnson and Brett Nagle for their help in compiling literature; Mel Warren for his support and countless hours of editing; and Tom Chart and Debra Felker for their time and effort in making available historical photographs of Colorado Pikeminnows in the archives of the Upper Colorado River Endangered Fish Recovery Program. Financial support was provided by the Department of Fisheries, Wildlife, and Conservation Biology and the Bell Museum of Natural History at the University of Minnesota.

Chapter 13

Catostomidae: Suckers

Phillip M. Harris, Gregory Hubbard, and Michael Sandel

Catostomids (order Cypriniformes) are commonly called Suckers because these fishes use their downward-directed mouths like vacuum cleaners to suck up small organisms, organic matter, and some detritus. The family name, Catostomidae, is derived from the Latinized Greek roots "kato," meaning "downward," and "stoma," meaning "mouth" (Boschung & Mayden 2004). Mullet is another name commonly applied to catostomids throughout North America, although that name refers to fishes in the family Mugilidae. Suckers inhabit a variety of freshwater ecosystems from large rivers and lakes to small headwater streams, making species of the family important functional components of aquatic habitats (e.g., Li et al. 1987; Schlosser 1987; Gido & Propst 1999; Clarkson & Childs 2000).

DIVERSITY AND DISTRIBUTION

Catostomidae consists of 12 genera and at least 76 recent species; 75 species of Suckers occur in North America (Table 13.1; Nelson et al. 2004). These 75 species constitute about 8% of the North American ichthyofauna with only minnows (Cyprinidae, Carps and Minnows) and darters (Percidae, Perches) having more species (Warren et al. 2000). The 2 most speciose genera are *Catostomus* (finescale Suckers, 26 species) and *Moxostoma* (redhorse and jumprock Suckers, 22 species), followed by *Ictiobus* (buffalofishes, 5 species), *Chasmistes* (lake Suckers, 4 species), *Carpiodes* (carpsuckers), *Erimyzon* (chubsuckers), *Hypentelium* (hog Suckers) and *Thoburnia* (torrent Suckers), each with 3 species, *Cycleptus* (blue Suckers, 2 species), and the monotypic genera *Deltistes* (*D. luxatus*, Lost River Sucker), *Minytrema* (*M. melanops*, Spotted Sucker), *Myxocyprinus* (*M. asiaticus*, Chinese Sucker), and *Xyrauchen* (*X. texanus*, Razorback Sucker). At least three genera, however, contain recognized undescribed species (e.g., *Catostomus*, Wall Canyon Sucker, Little Colorado River Sucker; *Cycleptus*, Rio Grande Blue Sucker; *Moxostoma*, Sicklefin Redhorse, Apalachicola Redhorse). In addition, several genera (e.g., *Catostomus*, *Carpiodes*, *Cycleptus*, *Ictiobus*, *Moxostoma*) have species showing evidence of polytypy. The Summer Sucker (*Catostomus utawana*), a former subspecies of White Sucker (*Catostomus commersonii*), is the most recently described species (Morse & Daniels 2009). Kettratad & Markle (2010) recognized the Tyee Sucker (*Catostomus tsiltcoosensis*) as a distinct species, resurrecting it from the synonomy of Largescale Sucker (*Catostomus macrocheilus*). Scharpf (2006) reviewed the described and undescribed taxa in Catostomidae.

One member of the family, the Harelip Sucker (*Moxostoma lacerum*), is particularly noteworthy because of its morphological distinctiveness and extinction in historical time. This species was described originally as *Lagochila lacera* on the basis of the unusual upper and lower lip morphology (Jordan & Brayton 1877; see morphology section). Although Jenkins (1970) regarded *Lagochila* as a terminal, derived offshoot within *Moxostoma*, G. R. Smith's (1992) phylogenetic hypothesis resolved *Lagochila* embedded within *Moxostoma*. This species was last collected in 1893, and only 33 specimens are deposited in ichthyological collections (Jenkins & Burkhead 1994). A phylogenetic hypothesis based on gene sequences might provide additional insights into the evolutionary relationships of this unique species, but unfortunately, current molecular methods cannot produce high-quality DNA from formalin-fixed specimens.

Table 13.1. Classification of extant Catostomidae (Suckers) (Harris & Mayden 2001; Harris et al. 2002). Number of species based on Nelson et al. (2004), in part. Information on intraspecific variation (number of species, number of subspecies) including references from Lee et al. (1981) and Scharpf (2006) unless noted. ? = no published study. Superscripted numbers refer to [1]Endemic to Yangtze and Minjiang Rivers in China (Gao et al. 2008); [2]Sun et al. (2004); [3]Kirsch (1889); [4]Jordan (1917); [5]Berendzen et al. (2003); [6]Jenkins (1970).

Subfamily	**Genus**	**Type Species**	**Number of Species**	**Number of Subspecies**	**Other Geographic or Phylogeographic Structure?**
Myxocyprininae	*Myxocyprinus* Gill 1878[1]	*Myxocyprinus asiaticus*	1		Yes[2]
Ictiobinae	*Carpiodes* Rafinesque 1820b	*Carpiodes cyprinus*	3	2	Yes
	Ictiobus Rafinesque 1820b	*Ictiobus bubalus*	5		Yes
Cycleptinae	*Cycleptus* Rafinesque 1819	*Cycleptus elongatus*	2		Yes
Catostominae					
Tribe Catostomini	*Catostomus* Lesueur 1817b	*Catostomus catostomus*	26	14	Yes
	Chasmistes Jordan 1878	*Chasmistes liorus*	4	2	No
	Deltistes Seale 1896	*Deltistes luxatus*	1		No
	Xyrauchen Eigenmann & Kirsch 1889[3]	*Xyrauchen texanus*	1		No
Tribe Erimyzonini	*Erimyzon* Jordan 1876	*Erimyzon oblongus*	3	4	?
	Minytrema Jordan 1878	*Minytrema melanops*	1		?
Tribe Thoburnini	*Thoburnia* Jordan and Snyder 1917[4]	*Thoburnia rhothoeca*	3		No
	Hypentelium Rafinesque 1818	*Hypentelium nigricans*	3		Yes[5]
Tribe Moxostomatini	*Moxostoma* Rafinesque 1820b	*Moxostoma anisurum*	22	2	Yes[6]

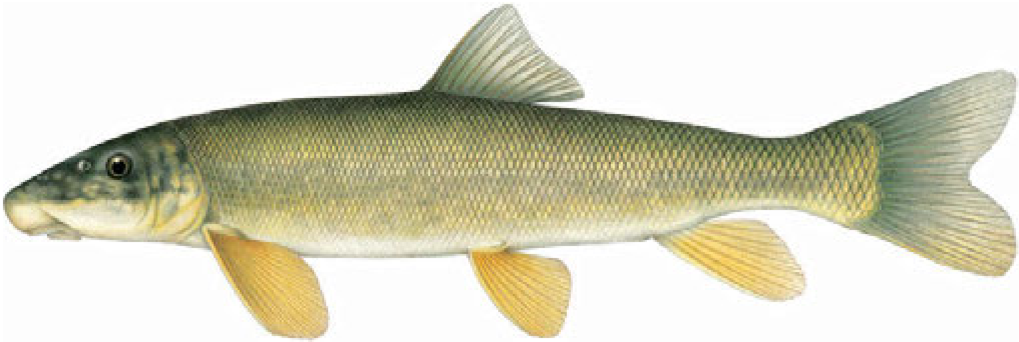


Plate 13.1. Longnose Sucker, *Catostomus catostomus*

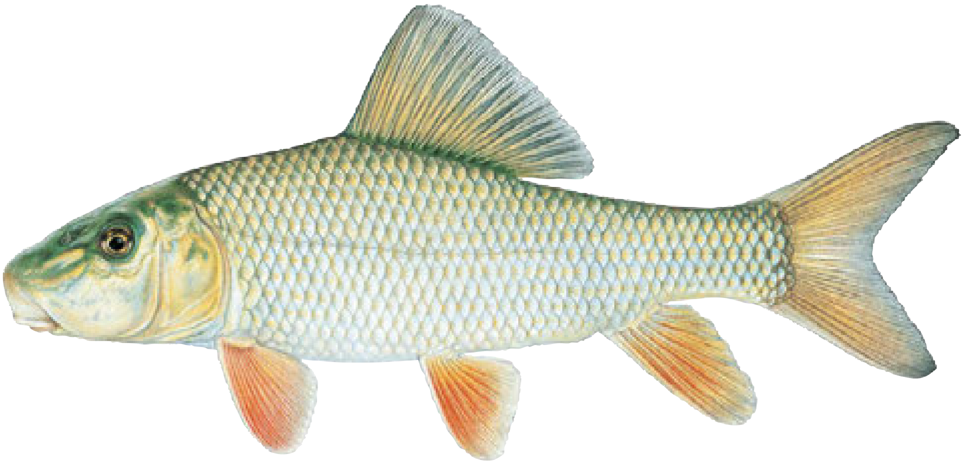


Plate 13.2. Silver Redhorse, *Moxostoma anisurum*

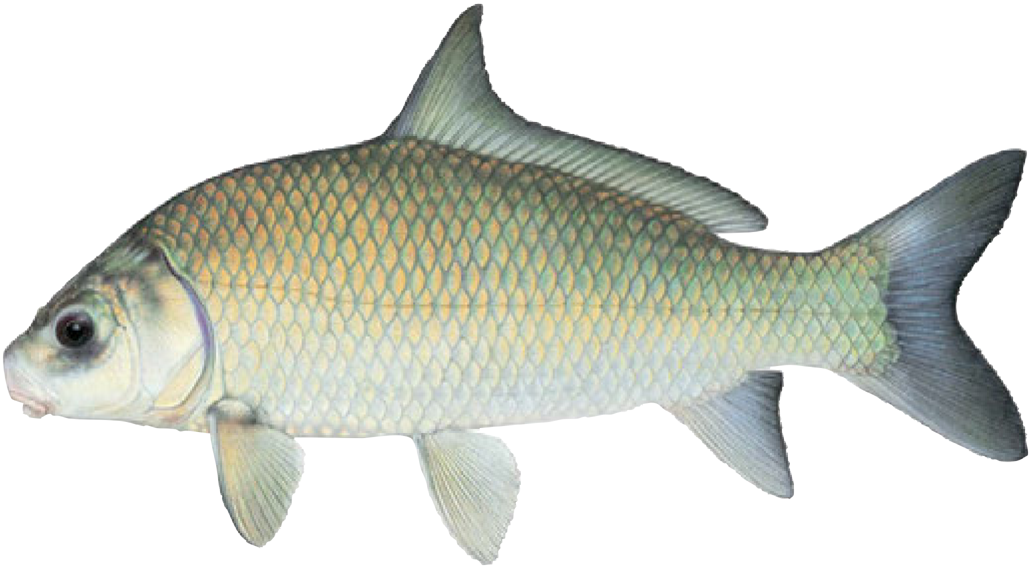


Plate 13.3. Smallmouth Buffalo, *Ictiobus bubalus*

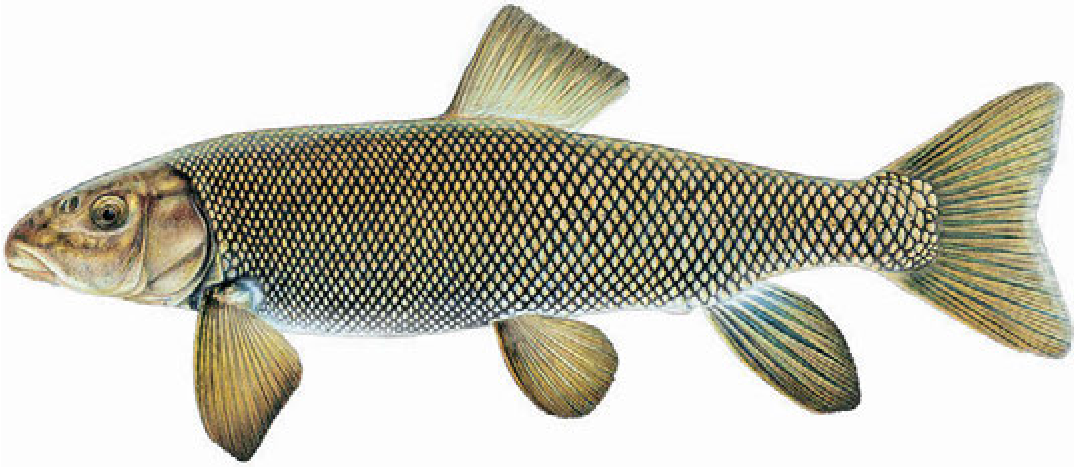


Plate 13.4. June Sucker, *Chasmistes liorus*

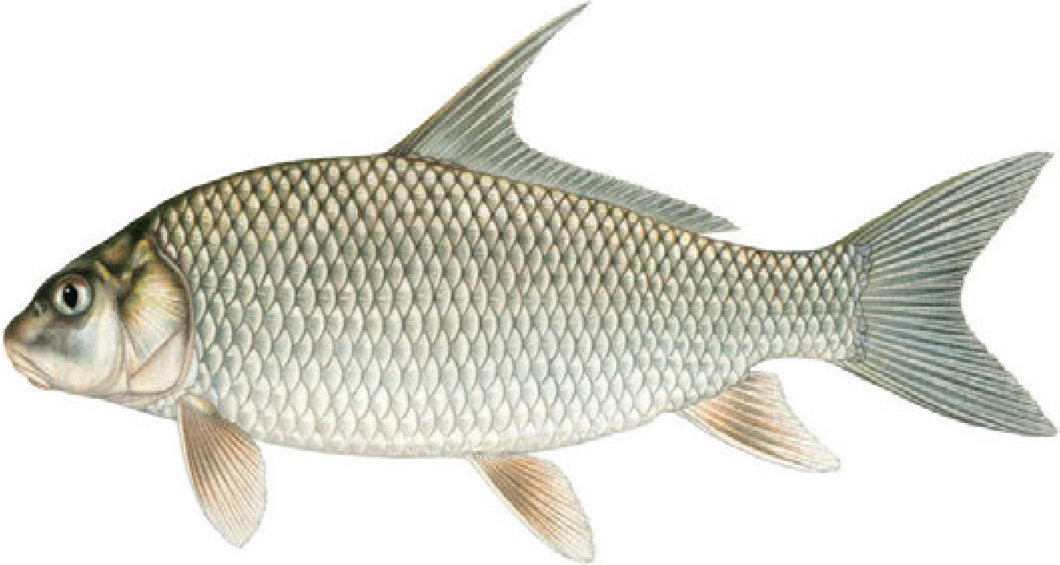


Plate 13.5. Quillback, *Carpiodes cyprinus*

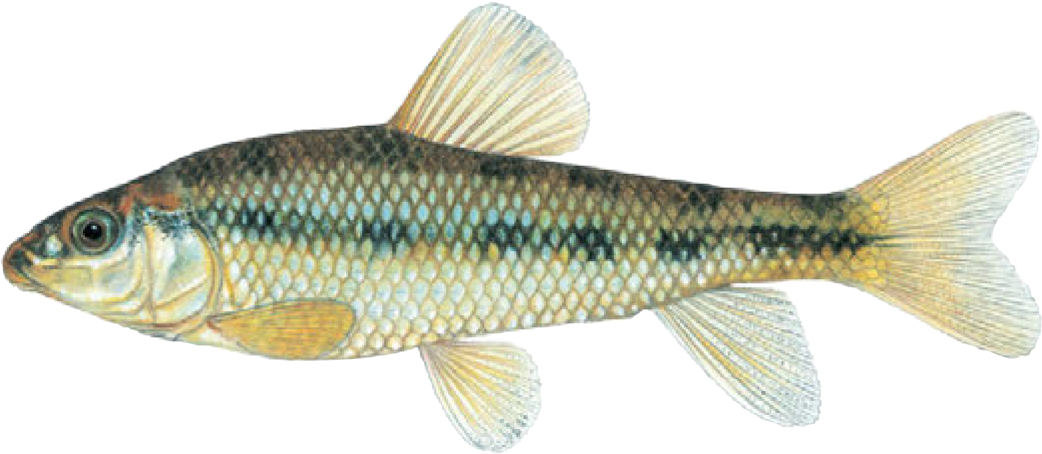


Plate 13.6. Creek Chubsucker, *Erimyzon oblongus*

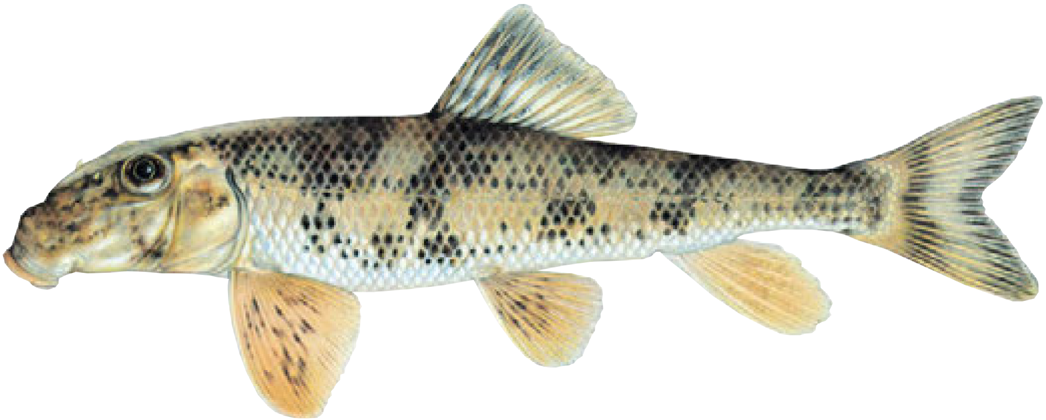


Plate 13.7. Northern Hog Sucker, *Hypentelium nigricans*

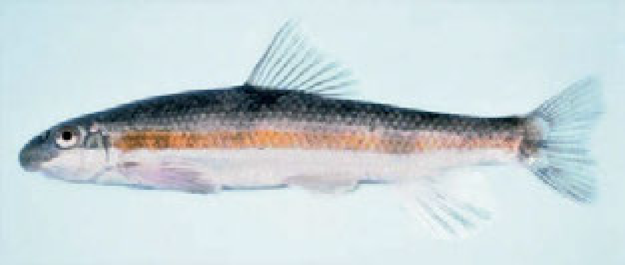


Plate 13.8. Torrent Sucker, *Thoburnia rhothoeca* (photograph by N. Burkhead and R. Jenkins, courtesy Virginia Department of Game and Inland Fisheries; used with permission from Noel Burkhead and the American Fisheries Society, copyright 1994)

Native Range

Suckers are Holarctic in distribution, but the family has a disjunct distribution between eastern Asia and North America. In eastern Asia, the Chinese Sucker (*Myxocyprinus asiaticus*) occurs in the Yangtse and Minjiang River drainages of eastern China (Gao et al. 2008); the Longnose Sucker (*Catostomus catostomus*) invaded eastern Siberia from Alaska during the last Pleistocene interglacial period (Berra 2001). Catostomids are widespread in North America with the northern limit being Arctic Ocean drainages (*C. catostomus*; Fig. 13.1) with the southern limit being the Rio Usumacinta of southeastern Mexico and northern Guatemala (*Ictiobus bubalus*, Smallmouth Buffalo; Lee et al. 1981; Berra 2001; Miller et al. 2005). The genera *Catostomus*, *Chasmistes*, *Deltistes*, and *Xyrauchen* occur west of the Continental Divide (Figs. 13.2–13.5), although two species, *C. catostomus* and *C. commersonii*, are distributed across much of northern North America (Lee et al. 1981). Most species diversity within *Catostomus* is associated with the complex, and often endorheic, basins of the western United States and northwestern Mexico. Several species of *Catostomus*, as well as *Chasmistes* and *Deltistes*, exhibit

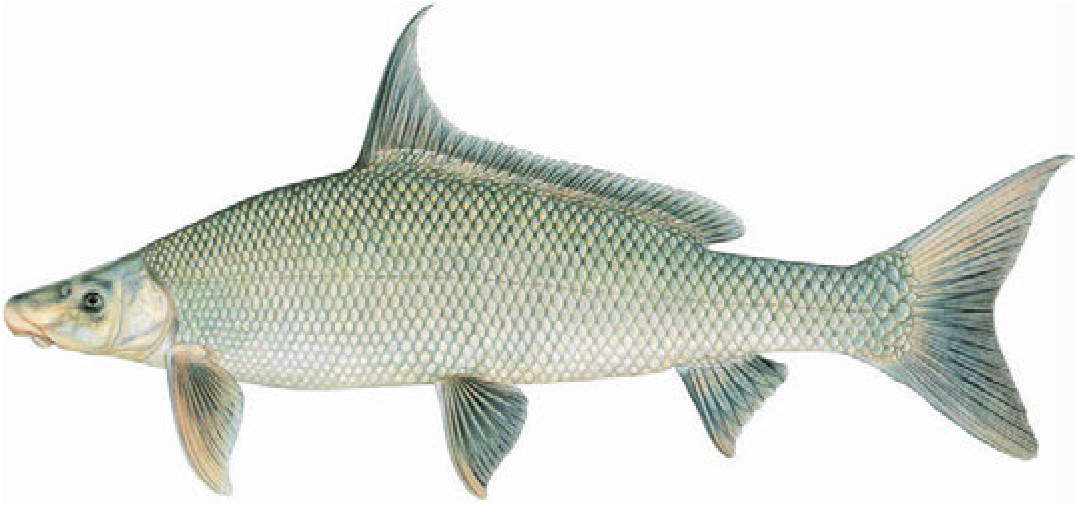


Plate 13.9. Blue Sucker, *Cycleptus elongatus*

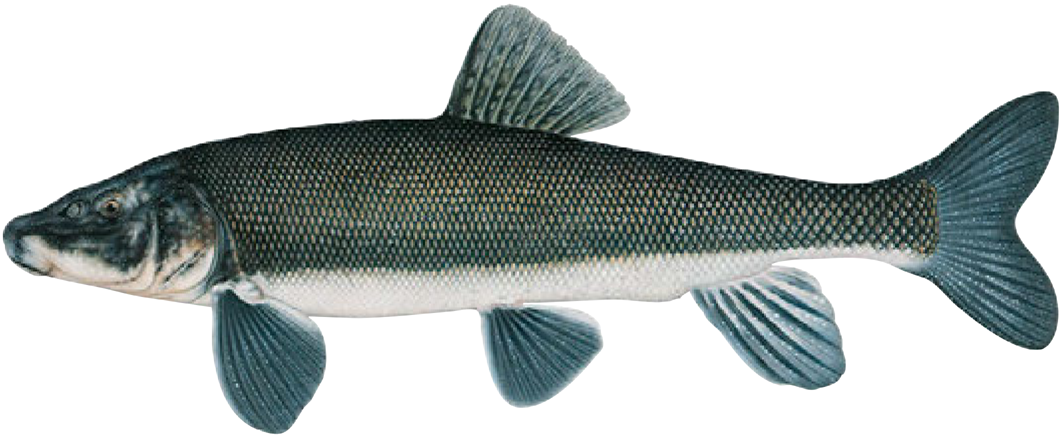


Plate 13.10. Lost River Sucker, *Deltistes luxatus*

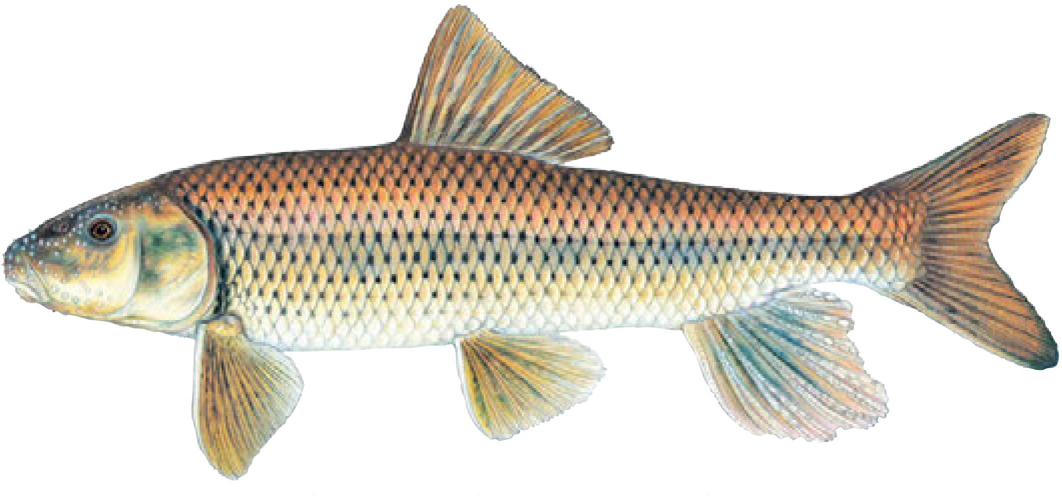


Plate 13.11. Spotted Sucker, *Minytrema melanops*

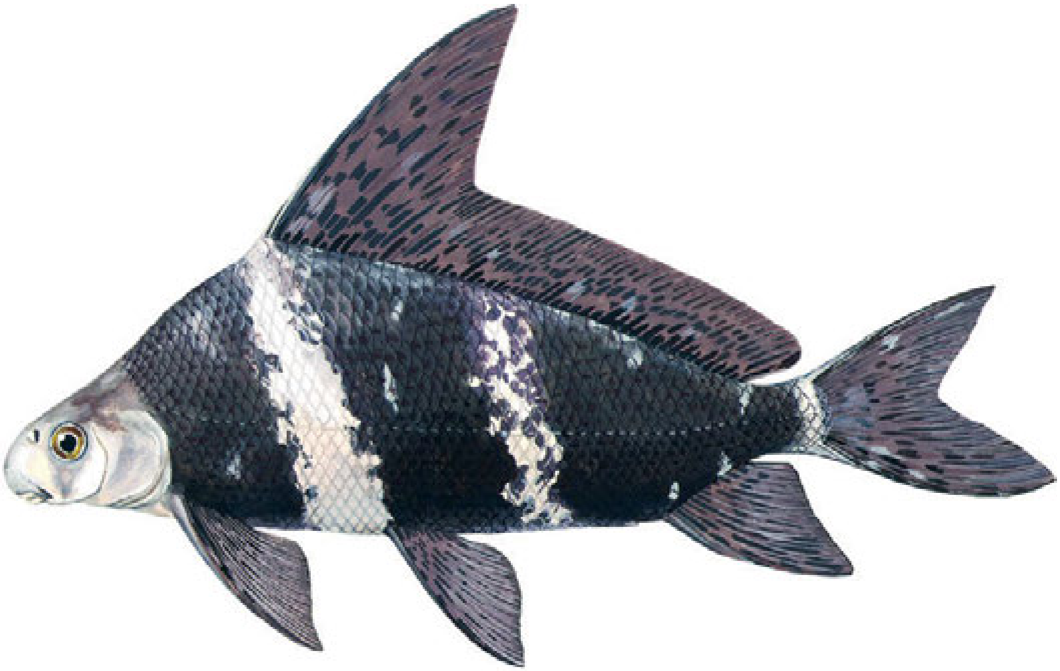


Plate 13.12. Chinese Sucker, *Myxocyprinus asiaticus*, juvenile (illustration used with permission of and copyrighted by Emily S. Damstra)

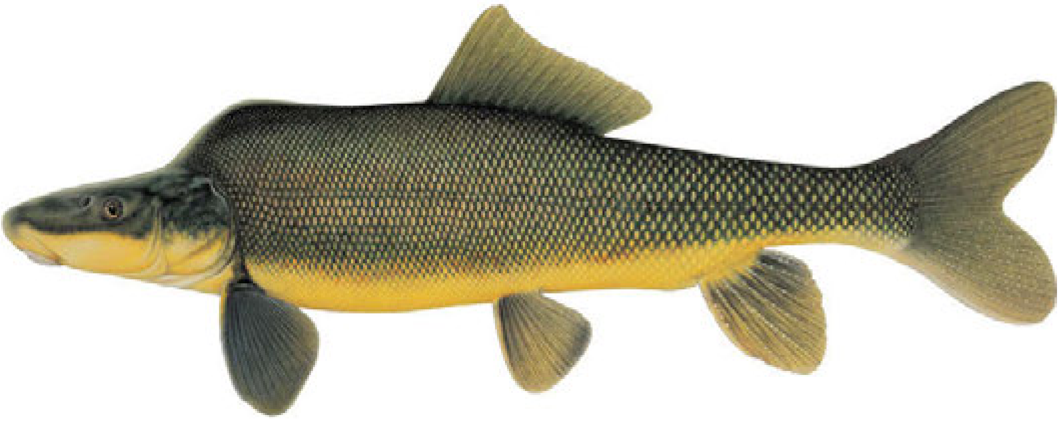


Plate 13.13. Razorback Sucker, *Xyrauchen texanus*

highly localized distributions and often are confined to a single basin. The Wall Canyon Sucker (*Catostomus* sp.) probably has the most limited distribution in the genus, occurring in a single stream system in northwestern Nevada. The monotypic genus *Xyrauchen* is endemic to the Colorado River basin (Fig. 13.5).

Suckers found primarily east of the western Continental Divide associated with large river systems (genera *Carpiodes*, Fig. 13.6; *Cycleptus*, Fig. 13.7; *Erimyzon*, Fig. 13.8; *Hypentelium*, Fig. 13.9; *Ictiobus*, Fig. 13.10; *Minytrema*, Fig. 13.11; and *Moxostoma*, Fig. 13.12) are more widespread in their distributions. Exceptions to this pattern are species of headwaters, small streams, or rivers (e.g., torrent Suckers, *Thoburnia*, Fig. 13.13; Roanoke Hog Sucker, *Hypentelium roanokense*; and jumprock Suckers, *Moxostoma*), which can exhibit highly localized distributions. Two species of *Moxostoma*, Mexican Redhorse (*Moxostoma austrinus*) and Mascota Jumprock (*Moxostoma mascotae*), occur on the Pacific Slope of Mexico.

Suckers as Non-Natives

Unlike some other families of North American freshwater fishes (e.g., Centrarchidae, Sunfishes; Salmonidae, Trouts

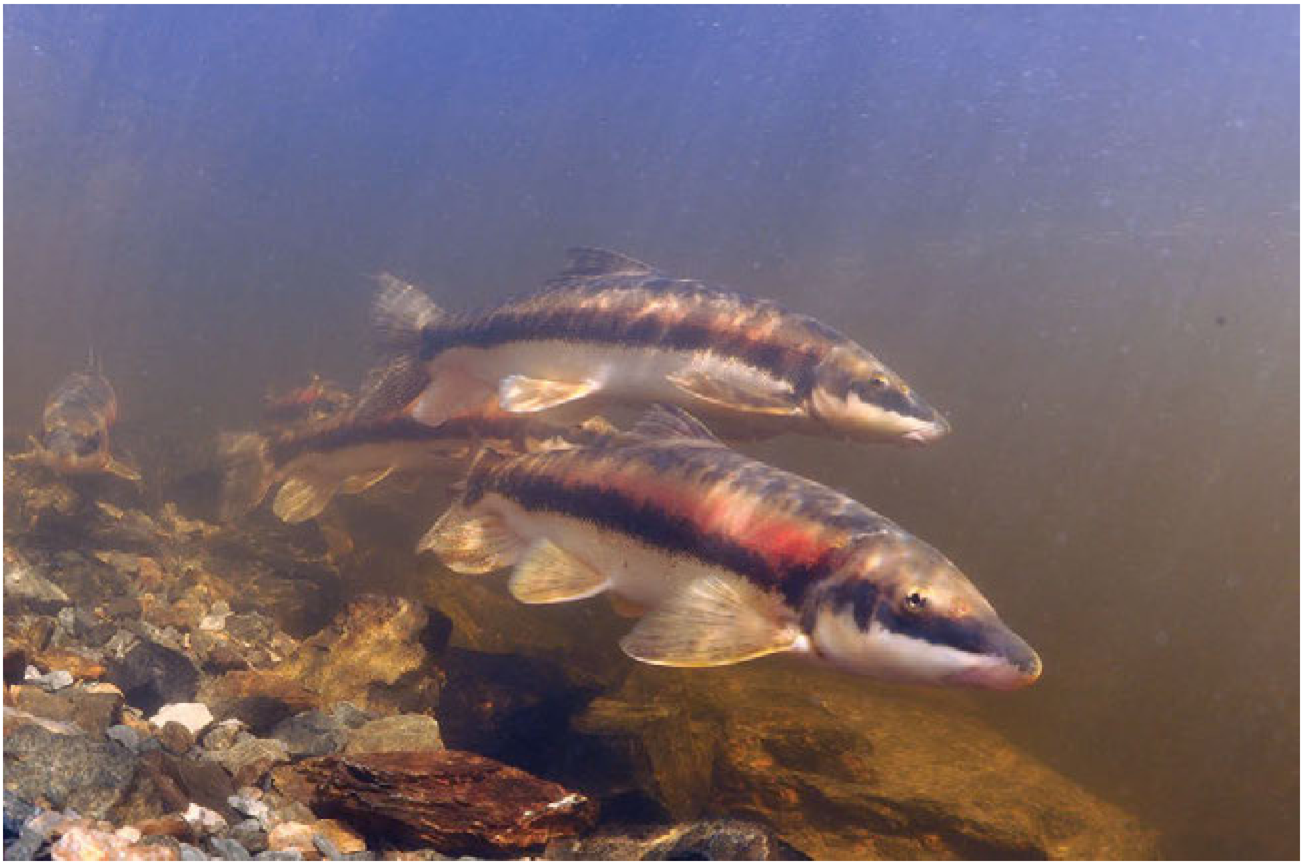


Figure 13.1. The Longnose Sucker, *Catostomus catostomus*, shown here cruising in a tributary to Great Slave Lake (Northwest Territories, Canada) in May 2012, is the most widespread species of Sucker (Catostomidae) in North America (Page & Burr 2011). The species ranges across Arctic, Pacific, and Atlantic Ocean drainages throughout Canada, Alaska, and much of the northern United States (photograph by and used with permission of ©Paul Vecsei / Engbretson Underwater Photography).

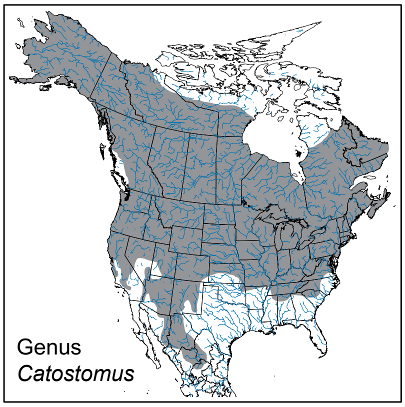


Figure 13.2. Geographic range of the genus *Catostomus*.

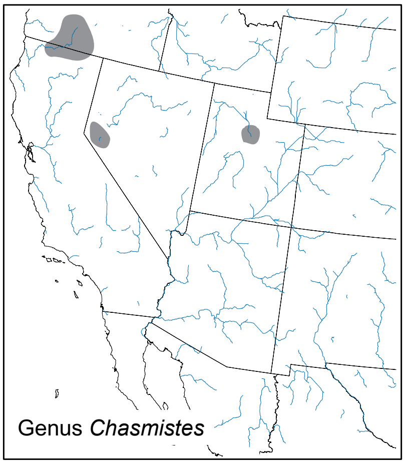


Figure 13.3. Geographic range of the genus *Chasmistes*.

and Salmons), catostomids have not been extensively introduced outside of North America. Most introductions were unsuccessful, in terms of establishing wild, reproductive populations, but a few exceptions exist. Only one introduction is thought to be associated with the ornamental fish industry. A single *C. commersonii* was collected in England not far from ornamental fish ponds containing Goldfish (*Carassius auratus*) imported from North Amer-

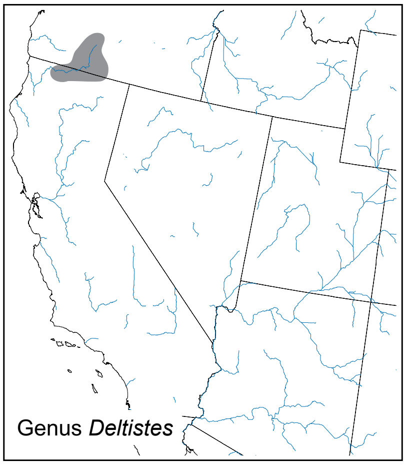

Genus *Deltistes*

Figure 13.4. Geographic range of the genus *Deltistes*.

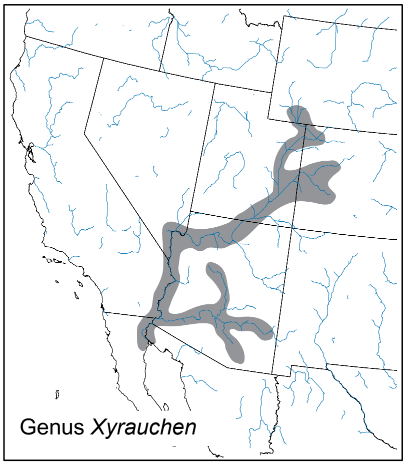

Genus *Xyrauchen*

Figure 13.5. Geographic range of the genus *Xyrauchen*.

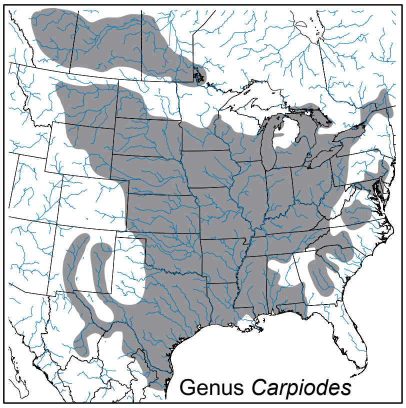

Genus *Carpiodes*

Figure 13.6. Geographic range of the genus *Carpiodes*.

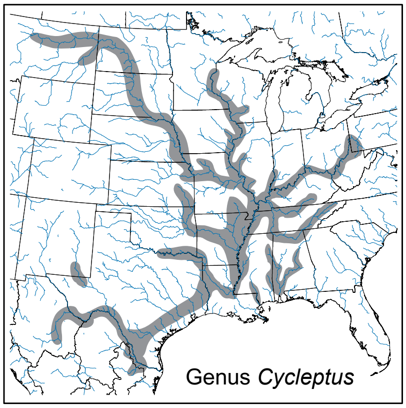

Genus *Cycleptus*

Figure 13.7. Geographic range of the genus *Cycleptus*.

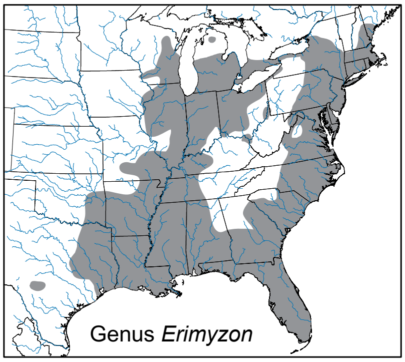

Genus *Erimyzon*

Figure 13.8. Geographic range of the genus *Erimyzon*.

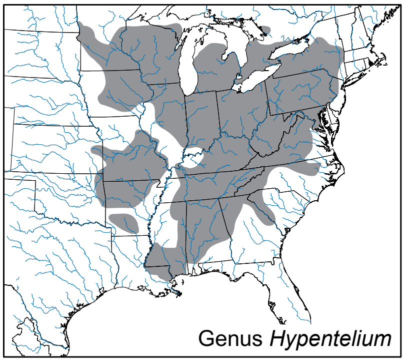

Genus *Hypentelium*

Figure 13.9. Geographic range of the genus *Hypentelium*.

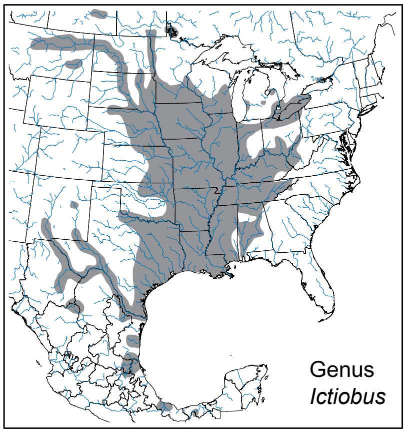

Genus
Ictiobus

Figure 13.10. Geographic range of the genus *Ictiobus*.

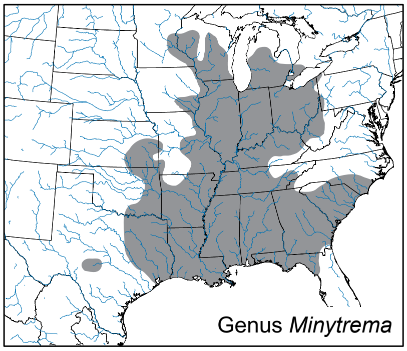

Genus *Minytrema*

Figure 13.11. Geographic range of the genus *Minytrema*.

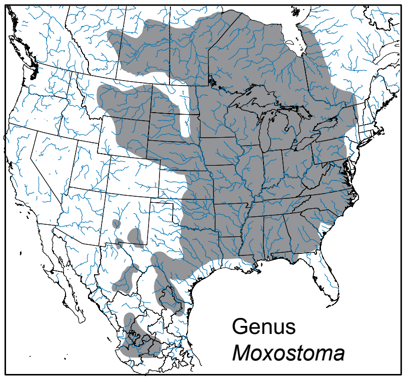


Figure 13.12. Geographic range of the genus *Moxostoma*.

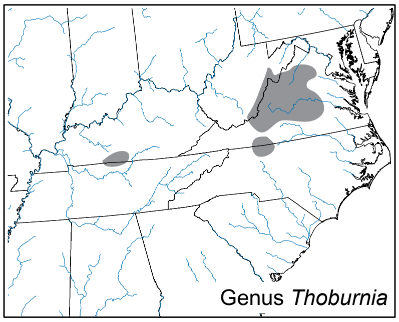


Figure 13.13. Geographic range of the genus *Thoburnia*.

ica (Copp et al. 1993); this specimen died shortly after collection.

The Quillback (*Carpiodes cyprinus*) and buffalofishes (*Ictiobus* spp.) have been introduced for aquaculture in eastern Europe, Central Asia, Israel, Mexico, Cuba, and Panama (Welcomme 1988). Introductions of the Quillback and Smallmouth Buffalo failed to establish reproductive populations in eastern Europe and Central Asia (Welcomme 1988). The Bigmouth Buffalo (*Ictiobus cyprinellus*) was introduced successfully into Russia, Cuba, and Panama (Makeyeav 1980). The Black Buffalo (*Ictiobus niger*) may be established in Central Asia because the population introduced into Cuba originated somewhere in the former Soviet Union (Welcomme 1988).

Introductions of Suckers outside their native ranges in North America are mostly associated with baitbucket transfers or accidental stocking with trout (*Oncorhynchus* spp.) into geographically proximate drainages (e.g., *Catostomus* spp.) or as forage fish (e.g., *Erimyzon* spp.; Fuller et al. 1999). Buffalofishes were stocked intentionally in Arizona in 1918 for sportfishing (Minckley 1973) and may have been transplanted subsequently into California by commercial fishers (Moyle 2002). Fuller et al. (1999) comprehensively reviewed catostomid introductions in North America.

PHYLOGENETIC RELATIONSHIPS

Higher Relationships

Before discussing phylogenetic relationships among catostomid lineages, it is worthwhile to briefly summarize previous works on the relationships of Catostomidae within the order Cypriniformes (Carps). A number of anatomical studies compared catostomids with other cypriniform taxa (Ramaswami 1957; see morphology section); Siebert (1987) and G. R. Smith (1992) reviewed historical works commenting on Catostomidae relationships.

Wu et al. (1981) presented the first cladistic examination of Cypriniformes relationships, although only Characiformes (Characins) were used as an outgroup. Although Catostomidae and Gyrinocheilidae (Algae Eaters) were depicted as sister-taxa, examination of character distributions indicates that no synapomorphies supported such a relationship. Two synapomorphies, however, did support an unresolved relationship among catostomids, gyrinocheilids, and cobitids (Loaches). Harris & Mayden (2001) resolved the Cobitidae (Loaches) as sister to a clade of Gyrinocheilidae + Catostomidae based on mtDNA 12S and 16S rDNA sequences, supporting Wu et al.'s (1981) hypothesis. One caveat associated with Harris & Mayden's (2001) analysis is limited taxon sampling among cypriniform fishes.

In contrast, both Sawada's (1982) analysis of the Cobitoidea (Cobitidae + Homalopteridae or Balitoridae, River Loaches) and Siebert's (1987) analysis of cypriniform relationships yielded the genus *Gyrinocheilus* as sister to a clade containing Catostomidae + Cobitidae and Homalopteridae. Both studies contain analytical weaknesses, including irreversibility of character evolution (Sawada) and limited number of transformation series examined (Siebert).

G. R. Smith (1992) provided the first, all-encompassing phylogenetic analysis of catostomid relationships. In methods, he discussed numerous morphological analyses supporting various cypriniform lineages as potential sister-taxa to catostomids. Despite examining numerous cypriniform taxa, however, only the genera *Leptobotia* (Cobitidae) and *Cyprinus* (Cyprinidae) were included as outgroups in his data matrix. Smith's phylogeny depicts a trichotomy among *Leptobotia*, *Cyprinus*, and Catostomidae, undoubtedly due to limited taxon sampling among potential outgroup taxa. Monophyly of catostomids, relative to *Leptobotia* and *Cyprinus*, is based on nine, "unique and unambiguous" morphological characters (G. R. Smith 1992:792): concave dorsal edge of opercle (two character states given for catostomids); detached cephalic sensory canals; fenestrate basioccipital process; small hyomandibular that articulates only with sphenotic; descending process of second and fourth pleural ribs of Weberian apparatus broadly sutured together; mandibular sensory canals lost; lateral ethmoid that is triradiate in longitudinal section; a porous, minute dermosphenotic; and 18 caudal rays. It would be interesting and informative to determine if these characters continue to diagnose catostomids with the inclusion of additional outgroup taxa.

Analyses based on molecular data sets offer contrasting phylogenetic hypotheses of relationships within Cypriniformes. Notably, all molecular analyses resolve Catostomidae as monophyletic, albeit with limited taxon sampling. Clements et al. (2004) examined growth hormone sequences; their analysis resolved a well-supported clade of Cobitidae sister to Catostomidae + Cyprinidae. This latter clade was also proposed by Uyeno and Smith (1972) based on karyotype data. Phylogenetic analyses of reduced (Harris & Mayden 2001; Tang et al. 2005) and complete (Saitoh et al. 2006) mitogenomic sequences consistently resolved Gyrinocheilidae sister to Catostomidae. In contrast, analyses of nuclear genes placed Catostomidae as either sister to remaining Cobitoidea + Cyprinoidea (Chen et al. 2009) or as sister to the Cobitoidea (Mayden et al. 2009); both analyses placed Gyrinocheilidae sister to remaining Cobitoidea.

Intrafamilial Relationships

Most early taxonomic and systematic efforts (pre-1900) on catostomids dealt with original descriptions and various contributions to higher-level classifications (reviewed by G. R. Smith 1992). Post-1900 contributions to catostomid classification include Hubbs (1930), who provided a key to eastern North American genera and designated tribes for these genera, and Robins & Raney's (1956) study of the genera and subgenera of *Moxostoma*. Nelson (1948, 1949) examined the Weberian apparatus and opercular series in catostomids; he concluded that these structures provided support for the subfamilial and tribal designations in Hubbs (1930). Miller (1959) presented a phylogeny of the Catostomidae that was based largely on Hubbs (1930) and Nelson (1948, 1949). In his discussion on relationships, Miller (1959:199) suggested that the Cycleptinae might be divided into two subfamilies consistent with the disjunct distribution of *Cycleptus* (North America) and *Myxocyprinus* (China). He depicted the Catostominae consisting of the Erimyzontini, genera *Erimyzon* + *Minytrema*, sister to Moxostomatini composed of *Moxostoma*, *Thoburnia*, *Hypentelium*, and *Lagochila* + Catostomini composed of *Catostomus*, *Pantosteus* (= *Catostomus*), *Chasmistes*, and *Xyrauchen*. Miller's hypotheses of relationships received support from Bussjaeger & Briggs (1978), who speculated on evolutionary affinities among catostomids based on bile salt chemistry. Jenkins's (1970) unpublished dissertation provided a comprehensive review of the taxonomy, classification, morphological variation, and distribution of the Moxostomatini; his was the first work to depict a phylogeny for the species in this tribe. Buth (1978, 1979, 1980) examined species-level relationships among *Hypentelium*, *Thoburnia*, and some species of *Moxostoma*. Ferris & Whitt (1978) constructed a phylogeny of 30 species based on the loss of duplicate gene expression in isozymes. Their Wagner tree placed the Ictiobinae sister to Cycleptinae + Catostominae. Within the Catostominae, they recognized three tribes, Erimyzonini, Moxostomatini, and Catostomini; *Moxostoma* was paraphyletic with *Moxostoma duquesnei* (Black Redhorse) sister to *Catostomus plebeius* (Rio Grande Sucker), *Catostomus platyrhyncus* (Mountain Sucker), and *Catostomus discobolus* (Bluehead Sucker).

As noted, G. R. Smith (1992) provided the first comprehensive analysis of catostomid relationships based on 64 taxa and 157 morphological, biochemical, and early life history transformation series. Smith's analysis produced 2 equally parsimonious trees of 852 steps (CI [confidence interval] = 0.35). In his preferred tree (Fig. 13.14) the Ictiobinae was sister to Cycleptinae + Catostominae, although Smith recognized that a limited number of characters supported this relationship. He also recognized the possibility of an Ictiobinae + Catostominae relationship based on a few homoplasious characters. Within the Catostominae, two tribes were recognized, the Catostomini and Moxostomatini. Within the Moxostomatini, Smith's analysis yielded a paraphyletic *Moxostoma* grade related to a paraphyletic *Scartomyzon* grade that, in turn, was related to a trichotomy of *Moxostoma ariommum* (as *Scartomyzon ariommus*, Bigeye Jumprock) + *Thoburnia* + *Hypentelium*. The second topology produced by this analysis had *Moxostoma cervinum* (as *Scartomyzon cervinus*, Blacktip Jumprock) as sister to *M. ariommum* (as *S. ariommus*) + *Thoburnia* + *Hypentelium*.

Harris & Mayden (2001) examined relationships among basal lineages of catostomids based on mtDNA 12S and 16S rDNA gene sequences (Fig. 13.15). These authors examined the influence of five structural classes (short and long stems, bulges, loops, unpaired bases) within the

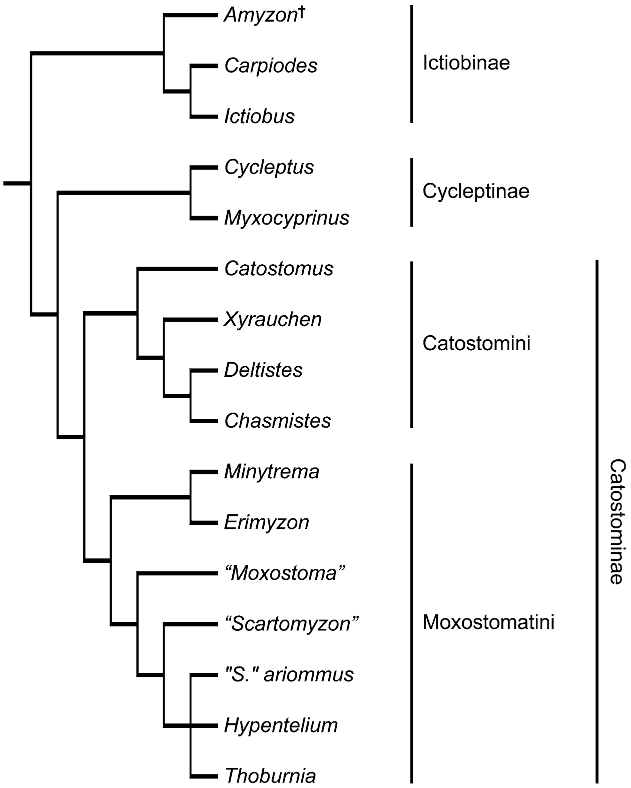

Amyzon†
Carpiodes
Ictiobus
Ictiobinae
Cycleptus
Myxocyprinus
Cycleptinae
Catostomus
Xyrauchen
Deltistes
Chasmistes
Catostomini
Minytrema
Erimyzon
"Moxostoma"
"Scartomyzon"
"S." ariommus
Hypentelium
Thoburnia
Moxostomatini
Catostominae

Figure 13.14. Phylogenetic hypothesis of relationships among catostomid lineages based on morphological, early life history, and biochemical characters (modified from G. R. Smith 1992).

rRNA secondary structure on sequence alignment and partitioned the data into these structural classes to examine rate heterogeneity and nucleotide substitution patterns. These molecular data consistently yielded a monophyletic Catostomidae, Ictiobinae, and Catostomini; the Catostominae was monophyletic in all analyses, except the 12S plus Valine 1:1 weighting analysis; the Moxostomatini was monophyletic in all combined and 16S analyses but was para- or polyphyletic in all analyses of the 12S + Valine data. The Cycleptinae was paraphyletic in all analyses, except the 12S + Valine 1:1 weighting analysis with *Myxocyprinus* as the basal-most taxon and the genus *Cycleptus* as either sister to remaining catostomids or sister to Catostominae (as in the majority of analyses). Within the Catostomini, relationships among species examined were not resolved; this is not surprising given the conservative nature of these two genes and the limited number of taxa examined.

Phylogenetic affinities of *Erimyzon* and *Minytrema* varied depending on the data set and weighting scheme; singly or together these two taxa were either sister to the Catostomini, sister to the Moxostomatini, or basal to a Catostomini + remaining Moxostomatini clade (Harris & Mayden 2001). Given the uncertain phylogenetic affinities of *Erimyzon* and *Minytrema* within the subfamily Catostominae, these taxa were identified as *incertae sedis*. Within the remaining Moxostomatini, the two species of *Scartomyzon* were resolved embedded within *Moxostoma*, questioning the monophyly of both *Moxostoma* and *Scartomyzon* if the latter genus is recognized as a distinct taxon. G. R. Smith (1992) noted that both *Moxostoma* and *Scartomyzon* formed paraphyletic grades (1992), suggesting that some species currently recognized in these genera may be more closely related to other *Moxostoma*, *Thoburnia* + *Hypentelium*, or form distinct evolutionary lineages.

To further examine phylogenetic relationships among the Moxostomatini, Harris et al. (2002) sequenced the entire mitochondrial cytochrome *b* gene from all species within this tribe and representative taxa from the Catostomini and other catostomid subfamilies. Maximum parsimony analysis of these gene sequences yielded two monophyletic clades: Catostomini (genera *Catostomus*, *Deltistes*, and *Xyrauchen*) + Erimyzonini (genera *Erimyzon*

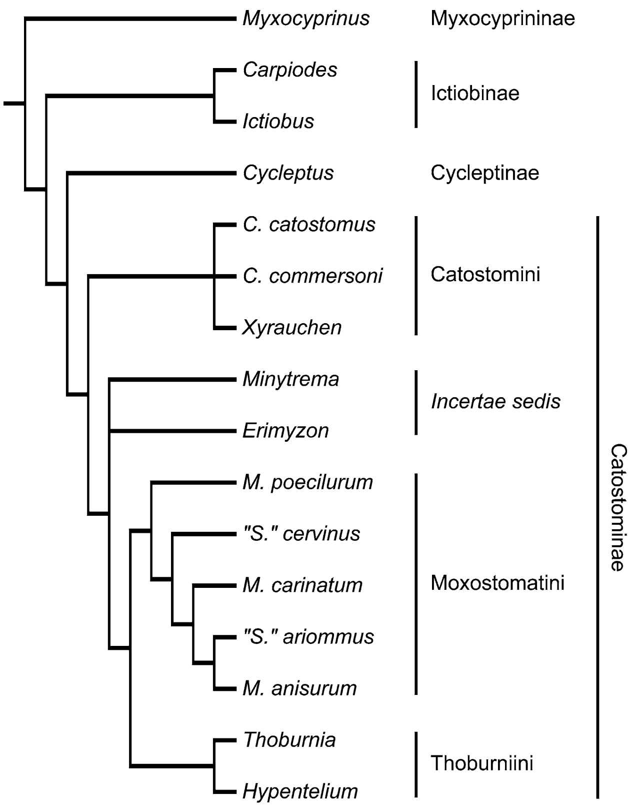

Myxocyprinus
Myxocyprininae
Carpiodes
Ictiobus
Ictiobinae
Cycleptus
Cycleptinae
C. catostomus
C. commersoni
Xyrauchen
Catostomini
Minytrema
Erimyzon
Incertae sedis
M. poecilurum
"S." cervinus
M. carinatum
"S." ariommus
M. anisurum
Moxostomatini
Thoburnia
Hypentelium
Thoburniini
Catostominae

Figure 13.15. Phylogenetic hypothesis of relationships among basal catostomid lineages based on mtDNA 12S and 16S rDNA gene sequences (redrawn from Harris & Mayden 2001).

and *Minytrema*); and Moxostomatini (genera *Moxostoma* and *Scartomyzon*) + Thoburniini (genera *Hypentelium* and *Thoburnia*). Within the Moxostomatini, the genus *Thoburnia* was either unresolved or polyphyletic; *Thoburnia atripinnis* (Blackfin Sucker) was sister to a monophyletic *Hypentelium* in the maximum likelihood analysis. In turn, these taxa were sister to a monophyletic clade containing the genera *Scartomyzon* and *Moxostoma*. The genus *Scartomyzon* was never resolved as monophyletic but was always recovered as a polyphyletic group embedded within *Moxostoma*, rendering the latter genus paraphyletic if *Scartomyzon* continued to be recognized. Relationships among lineages within the *Moxostoma* and *Scartomyzon* clade were resolved as a polytomy.

Sun et al. (2007) presented a UPGMA (unweighted pair group method with arithmetic mean) tree based on mitochondrial cytochrome *b* for 17 species of catostomids. Their results are somewhat at odds with previous studies. Although Catostomidae was monophyletic, the genus *Minytrema* was the basal-most taxon. A paraphyletic Cycleptinae (sensu G. R. Smith 1992) was sister to a monophyletic Ictiobinae; this clade was, in turn, sister to Catostominae, minus the genus *Minytrema*. Within the Catostominae, the genus *Erimyzon* was sister to a clade containing a monophyletic Moxostomatini + a non-monophyletic Catostomini, due to the genus *Thoburnia* being embedded in this tribe. Although there is some concordance between the results of this and previous studies, limited taxon sampling and analytical issues in this paper limit the value of Sun et al.'s (2007) hypothesis.

Doosey et al. (2009) used mitochondrial ND 4/5 sequences to infer phylogenetic relationships within the family with more complete taxon sampling than in previous studies. Relationships among basal catostomid lineages differed from previous hypotheses in that a clade consisting of Cycleptinae sister to Myxocyprininae + Ictiobinae was sister to Catostominae. Within Catostominae, the Erimyzonini was sister to a clade containing the Catostomini sister to Moxostomatini + Thoburnini. Species-level groupings recovered within the Moxostomini were similar to those of Harris et al. (2002), although their data provided better resolution to relationships among lineages. Depending on the coding scheme used in the sequence analyses, some species-level relationships received moderate to low bootstrap support in the maximum likelihood analyses. Thus, the most recent published phylogenetic examination of relationships within the Moxostomatini emphasizes the need for additional character data (either molecular or morphological) to clarify relationships among these lineages.

FOSSIL RECORD

Suckers are represented in the fossil record of North America and Asia dating from the Eocene (55–35 mya; Smith 1981; Cavender 1986; Sytchevskaya 1986; Chang et al. 2001; Liu & Chang 2009). Fossil catostomids often occur in lacustrine or palustrine sediments in association with fossil Bowfin (Amiidae), Pikes (Esocidae), and Catfishes (Siluriformes) (Cope 1884; Grande et al. 1982; Chang & Maisey 2003). Co-occurrence with minnow (Cyprinidae) fossils is less common and is observed primarily in Miocene-Age deposits (25–5 mya; Cavender 1986).

North American fossil deposits from the Eocene have produced a wealth of information on the paleoecology of catostomids. Suckers are often the most abundant fossils at a given locality, and some deposits yielded enough specimens to estimate growth rates and year-class abundances from size-frequency data (Wilson 1984). Paleoichthyological studies have examined large-scale die-offs of freshwater fishes in the western United States. Hypoxia was the most likely cause of death among specimens of the extinct castomid genus †*Amyzon*, based on the recovery of well-articulated skeletons with gaping mouths (Barton & Wilson 2005). In contrast, relatively few extinctions occurred during the Late Cenozoic among eastern North American taxa, primarily due to the long-term geological stability of the region and the north-to-south orientation of many drainages that provided access to southern refuges during the glacial advances of the Pleistocene (2.6–0.01 mya; Smith 1981).

Fossil catostomids from the Eocene include the genera †*Amyzon* Cope 1872, †*Vasnetzovia* Sytchevskaya 1986 (both ictiobines, or carpsuckers and buffalofishes), and †*Plesiomyxocyprinus* Liu and Chang 2009 (a myxocyprinin in the same lineage as the Chinese Sucker). The genera †*Vasnetzovia* and †*Plesiomyxocyprinus* are restricted to East Asia, thus far; the genus †*Amyzon* occurs in East Asia and western North America. Putative catostomid fossils from the Paleocene Paskapoo Formation of Alberta (Wilson 1980) can only be identified reliably as cyprinoids (Cavender 1991). Fossils of modern Sucker genera are found in Middle to Late Miocene (about 16–5 mya) deposits (Cavender 1986; Chang et al. 2001). Fossils from Pleistocene-Age deposits are "osteologically indistinguishable" from extant species (Grande et al. 1982:523).

The genus †*Amyzon* is probably not monophyletic (Wilson 1984; Cavender 1986). In body form, †*Amyzon* generally resembles a miniaturized form of *Carpiodes*, having a deeply compressed body and an elongate dorsal fin base.

This genus is diagnosed by the absence of an intercalar, an anteriorly directed premaxillary process, an intermediate (as opposed to broad or sharp) pterotic ridge, five or more infraorbitals, scales with sharp anterolateral corners, and a short, broad dermethmoid spine (Miller & Smith 1981; G. R. Smith 1992). †*Amyzon*-like forms existed for ≥20 million years in North America; the most recent fossils are estimated to about 31 million years old (Evernden & James 1964; Cavender 1986).

The number of species within †*Amyzon* depends on interpretation of variation in meristic and morphometric characters, which are notoriously variable among extant Catostomidae. Adding to the taxonomic confusion, many species are described from small or incomplete fossil remains. Some characters originally used for species descriptions are now attributed to clinal variation or sexual dimorphism (Lambe 1906; Wilson 1984). Cope (1872) described the type species, †*A. mentale*, from the Osino Oil Shales of Eocene-Oligocene Nevada (56–23 mya). Cope (1874, 1875) also described three additional species from the Florissant Formation of Colorado: †*A. commune*, †*A. pendatum*, and †*A. fusiforme*. Of these three species, only †*A. commune* is still recognized as a valid species (Bruner 1991a). Bruner (1991a) also considered †*A. gosiutensis* (Grande et al. 1982) from the Eocene Green River Formation in Wyoming to be a junior synonym of †*A. aggregatum* (Wilson 1977) from British Columbia, despite the great geographic separation between the two localities. †*Amyzon brevipinne* (Cope 1893) was the first Sucker to be described from the productive fossil beds of Eocene British Columbia. Additional species of †*Amyzon* remain undescribed from deposits of British Columbia and other areas of North America (Bruner 1991a). These North American fossils are part of a rich, Holarctic †*Amyzon* fauna of which the most recently described, or redescribed, species are from Asia. Chang et al. (2001) described †*A. hunanensis* from Hunan Province in southern China and discussed how fossils originally described as minnows, but subsequently identified as Suckers, have expanded the distribution of fossil catostomids in Asia. As yet, it is unclear whether species of †*Amyzon* ever co-occurred with extant ictiobine genera.

The oldest fossils of extant genera ostensibly belong to species of *Ictiobus* from the Middle Miocene (16–12 mya) strata of South Dakota (Cavender 1986). Putative records of ictiobine fossils from Oligocene (34–23 mya) deposits in Kazakhstan were refuted (but see G. R. Smith 1992). Pliocene-Age (6–2.5 mya) ictiobines include †*Ictiobus aguilerai*, described from Hidalgo, Mexico (Alvarado-Ortega et al. 2006), as well as fossils of extant species, such as *I. bubalus* from Oklahoma (G. R. Smith 1962). Pleistocene-Age beds have yielded *I. cyprinellus* from Nebraska (Smith & Lundberg 1972), *I. niger* from Kansas (Neff 1975), and assemblages of other ictiobines from Texas (Uyeno & Miller 1962; Lundberg 1967), Michigan, and Montana (Smith 1981; Cavender 1986).

Fossils of taxa in the subfamily Catostominae are generally more recent in age, but in the western United States a substantial fossil record for *Chasmistes* confirms their presence by the Late Miocene (12–5.5 mya; Smith 1975; Miller & Smith 1981); *Xyrauchen texanus* is known from Pliocene-Age deposits (Hoetker & Gobalet 1999). An extensive fossil record exists for *Chasmistes*, *Catostomus*, and *Deltistes* from Plio-Pleistocene-Age deposits (6–0.01 mya) from the western United States (Smith 1981). Fossil-rich deposits containing catostomids include Fossil Lake, Idaho, Glenns Ferry Formation, Utah, Cabbage Patch fauna, Montana, and many others in South Dakota, Nebraska, Oregon, and California (Miller & Smith 1967; Smith 1975; Cavender 1986). Fossils for eastern North American Suckers are generally known from Late Pleistocene deposits (1.8–0.01 mya), but fossil *Minytrema melanops* and Silver Redhorse (*Moxostoma anisurum*) were recovered from Early and Middle Pleistocene deposits (2.5–1.8 mya) in Kansas and around the Great Lakes (Cleland 1966; Eshelman 1975). A potentially new species of fossil redhorse (*Moxostoma*) is known from the Lake Chapala Basin, Jalisco, Mexico (Smith et al. 1975; Miller 1986).

MORPHOLOGY

General Morphology

Catostomidae is a diverse family of fishes, exhibiting great variation in body shape and size. In general appearance, Suckers resemble large minnows (Cyprinidae), although large-river species tend to be deep-bodied, almost stocky or chunky in appearance (e.g., the genera *Carpiodes* and *Ictiobus*), and stream-dwelling Suckers are more elongate than most North American minnows. Some of the most unusual body shapes in freshwater fishes occur in juvenile *Myxocyprinus asiaticus* and *Xyrauchen texanus*, both of which have enlarged nuchal areas that might function as adaptations for living in fast-flowing, large rivers or as an anti-predator defense (see Portz & Tyus 2004). The enlarged nuchal hump of *Xyrauchen* is modified further into a sharp keel; *Xyrauchen* literally translates as “razor nape” (Minckley 1973). Interestingly, the nuchal hump of

Myxocyprinus becomes less pronounced with growth, and in a mature adult, the body somewhat resembles that of *Cycleptus* (Fig. 13.16).

In addition to similar body shape, Suckers and minnows also have a single dorsal fin, a scale-less head, and cycloid scales. Suckers can be differentiated from North American minnows based on a single dorsal fin with ≥10 fin rays, a more posteriorly placed anal fin, 18 principal caudal fin rays, barbels conspicuously absent from around the mouth, and in most species an inferior, highly protrusible mouth with plicate or papillose lips. Other external features of catostomids, such as pigmentation and meristic and mensural characters, are described and illustrated in many state fish books (Etnier & Starnes 1993; Jenkins & Burkhead 1994; Boschung & Mayden 2004).

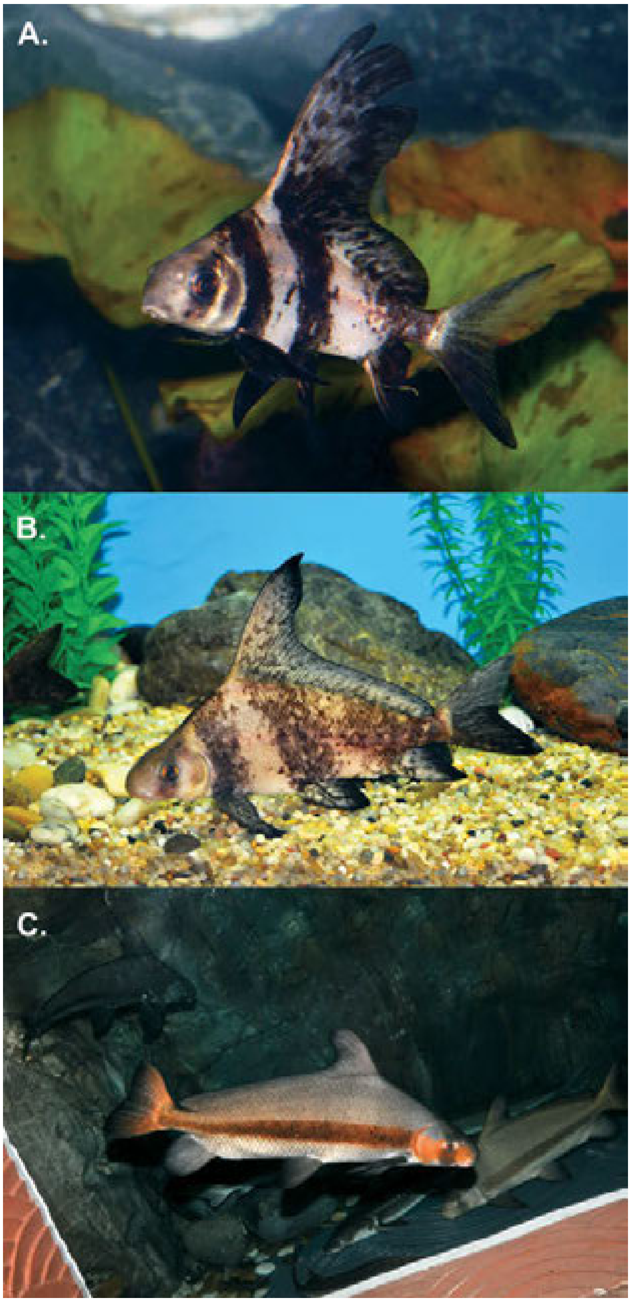


Figure 13.16. (A) Juvenile, (B) semi-adult, and (C) adult Chinese Suckers, *Myxocyprinus asiaticus*. Juvenile and semi-adult from Yangtze River, Hunan Province, China. Adult photographed in the Shanghai Ocean Aquarium (photographs by and used with permission of N. Khardina, juvenile, and H. Bleher, semi-adult and adult, Aquapress Publishers, Italy, www.aquapress-bleher.com,copyright 2009).

Catostomids probably originated as large-bodied riverine fishes, and subsequently radiated and adapted to lower-order, higher-gradient streams by becoming increasingly smaller in body size (G. R. Smith 1992). This trend is clearly seen when comparing body sizes of the large river or lake Suckers (genera *Carpiodes*, *Cycleptus*, *Deltistes*, *Ictiobus*, *Myxocyprinus*, and *Xyrauchen*) that can grow to be >60 cm TL (Etnier & Starnes 1993; Baensch & Riehl 1995; Moyle 2002; Boschung & Mayden 2004) with some headwater populations of *Hypentelium roanokense*, which are ≤14 cm TL (Jenkins & Burkhead 1994), and other dwarf forms of *Catostomus* (e.g., Salish Sucker, *Catostomus* sp., about 29 cm FL, Pearson & Healey 2003; Jenny Creek population of the Klamath Smallscale Sucker, *Catostomus rimiculus*, 21 cm SL, Hohler 1981). Based on weight, the largest Sucker caught in a sport fishery appears to be a 40 kg *Ictiobus bubalus* taken from Lake Wylie, North Carolina (NCWRC 2010).

Mouth and Lip Morphology

The morphology of the mouth and lips in Suckers is undoubtedly their most distinctive feature. Although the mouth and lips of a few species of minnows in North America might superficially resemble those of catostomids (e.g., cyprinid genera *Campostoma* and *Phenacobius*), none have lips so fully developed as those of some Suckers. As with other morphological characters, however, a great deal of variation in lip morphology is exhibited by catostomids. The general tendency, however, is for large-river and lake Suckers (e.g., genera *Carpiodes*, *Chasmistes*, *Deltistes*, *Erimyzon*, *Ictiobus*, *Minytrema*, *Xyrauchen*) to have less well-developed lips and lip texturing (see following paragraph) than small river– or stream-inhabiting forms; an exception is the genus *Cycleptus*, species of which frequent large rivers and have big lips and well-developed lip papillae (Burr & Mayden 1999:39).

Jenkins & Burkhead (1994) classified the morphology of lip textures in some catostomids into character states.

They recognized five character states of lip textures: plicate (Fig. 13.17a)—the lips appear to have longitudinal grooves or pleats; subplicate (Fig. 13.17b, lower lip)—the lips are similar to plicate ones, but individual grooves can be divided into smaller sections; plicate-papillose (Fig. 13.17c)—the lip texture is a mix of plicae and papillae; papillose—numerous papillae cover the lips, resembling small, round bumps (Fig. 13.17d) or are raised and elongated resembling villi (see also Rio Grande form of *Cycleptus elongatus*, Blue Sucker; Burr & Mayden 1999); and semipapillose (Fig. 13.17f)—the plicae are oval or oblong, not columnar, in appearance, and the papillae are not raised. As noted previously, *Moxostoma lacerum* has unusual lips for a catostomid (Fig. 13.17g). The upper lip is hood like, and the lower lip is cleft into two distinct lobes; lip texturing is lightly papillose with a small number of plicae on the posterior edge of the upper lip (Jordan & Brayton 1877; Etnier & Starnes 1993; Jenkins & Burkhead 1994). The plicae are more pronounced in juveniles than in small adults (Etnier & Starnes 1993).

Lip morphology and texturing are related directly to external brain morphology as revealed by an examination of 46 species of catostomids (Miller & Evans 1965). Taste in catostomids occurs either from taste buds on the lips and skin or in the mouth and pharynx. The facial lobe of the brain receives sensory input from taste buds on the lips and skin, and the vagal lobe receives such input from taste buds in the mouth and pharynx. Not surprisingly, species with large, papillose lips, have larger facial lobes, including, e.g., the genera *Cycleptus*, *Hypentelium*, *Thoburnia*, and some *Moxostoma* and *Catostomus* (*Pantosteus*). In contrast, those species with smaller lips and less texturing (e.g., genera *Carpiodes*, *Ictiobus*, *Erimyzon*, various species of *Moxostoma* and *Catostomus*) have larger vagal lobes.

Pigmentation and Breeding Tubercles

Coloration of Suckers tends to be rather drab when compared with that of other North American freshwater fishes such as Sunfishes, some minnows, and most darters, but even so, a great deal of variation exists among the genera. Colors in adults range from an almost uniform silvery across the body (e.g., *Carpiodes* spp.) to a dark olive or brown or brassy dorsally, fading to a light yellow or white ventral surface (Etnier & Starnes 1993; Jenkins & Burkhead 1994; Moyle 2002). The genera *Cycleptus* and *Deltistes* are dark blue to almost black across the back and sides with a light-colored ventral surface (Moyle 2002; Boschung & Mayden 2004). In contrast to the more uniform body coloration noted above, the genus *Hypentelium* has dark, dorsal saddles and blotches on the sides (Etnier & Starnes 1993; Boschung & Mayden 2004). The Spotted Sucker and

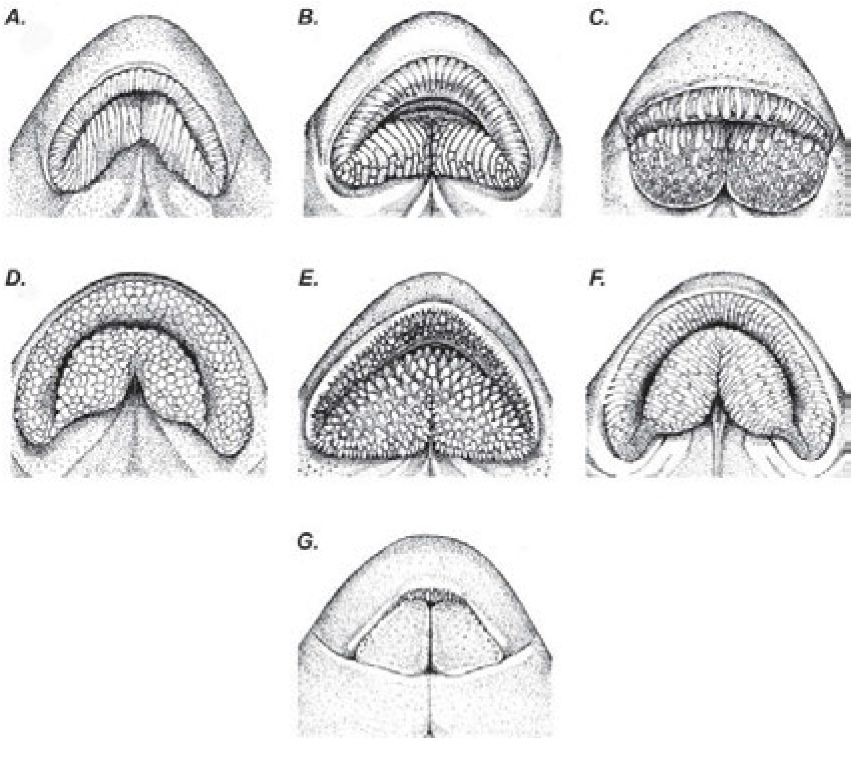


Figure 13.17. Lip morphology in suckers: (A) plicate, Golden Redhorse, *Moxostoma erythrurum*; (B) subplicate, Shorthead Redhorse, *M. macrolepidotum*; (C) plicate-papillose, Rustyside Sucker, *Thoburnia hamiltoni*; (D) papillose, Northern Hog Sucker, *Hypentelium nigricans*; (E) papillose, Bigeye Jumprock, *M. ariommum*; (F) semipapillose, Silver Redhorse, *M. anisurum;* and (G) Harelip Sucker, *M. lacerum* (illustrations from Jenkins & Burkhead 1994, and reproduced with permission from the American Fisheries Society).

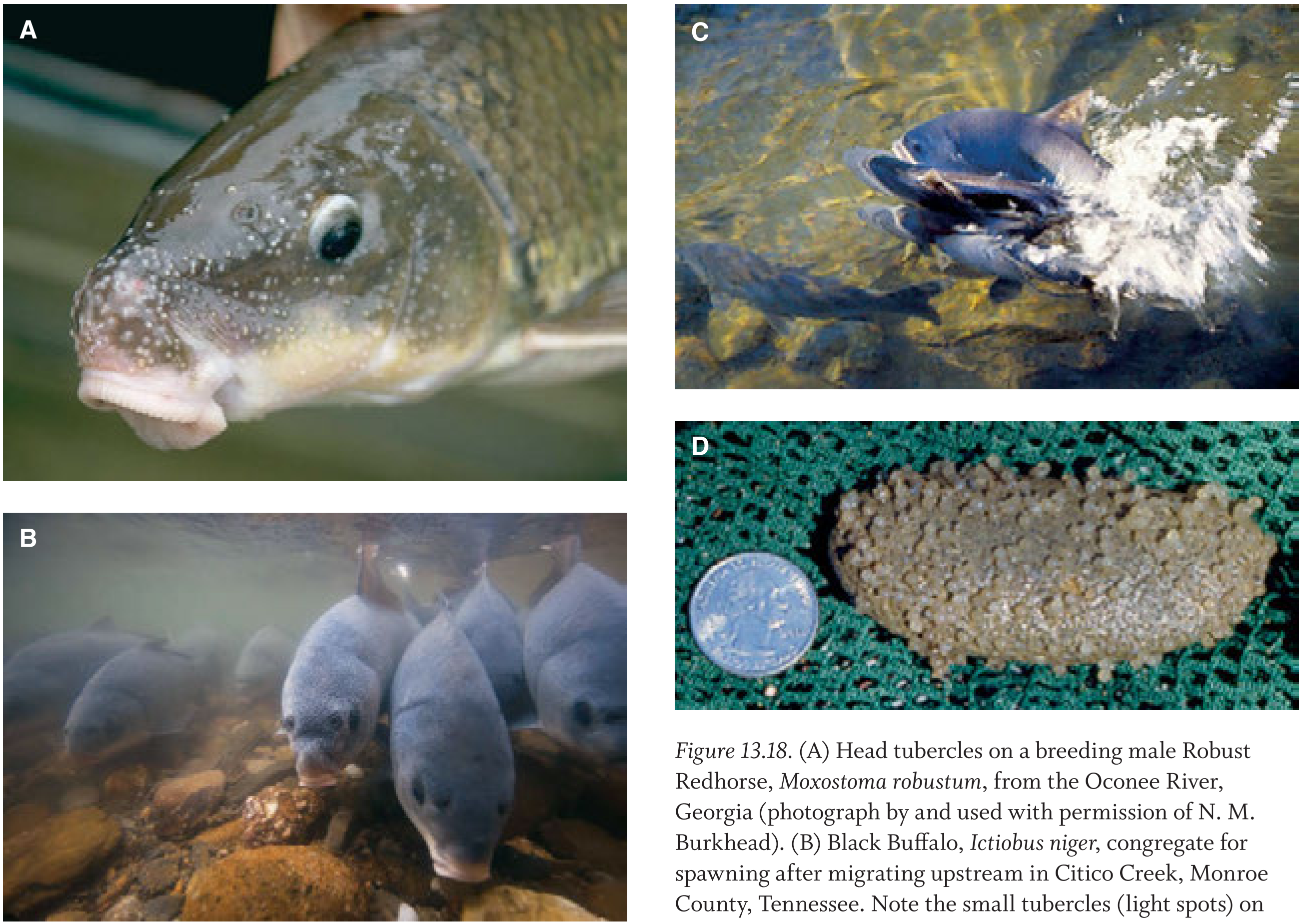


Figure 13.18. (A) Head tubercles on a breeding male Robust Redhorse, *Moxostoma robustum*, from the Oconee River, Georgia (photograph by and used with permission of N. M. Burkhead). (B) Black Buffalo, *Ictiobus niger*, congregate for spawning after migrating upstream in Citico Creek, Monroe County, Tennessee. Note the small tubercles (light spots) on the male in the center of the photograph (photograph by and used with permission of Dave Herasmitschuk, Freshwaters Illustrated). (C) A female Black Buffalo is sandwiched between two males as the three churn the surface of the water during a spawning bout in Citico Creek (photograph by and used with permission of Kyle Piller). (D) Eggs of the Black Buffalo adhering to a rock in Citico Creek (photograph by and used with permission of Kyle Piller).

Blackfin Sucker have dorsal and lateral stripes, although the stripes in the Spotted Sucker are formed by dark spots at the base of the scales (Etnier & Starnes 1993; Boschung & Mayden 2004). In many species, the fins are often colored orange or red and become especially vivid in nuptial individuals. The coloration of juveniles is often quite distinct from that of adults. For example, juvenile Blue Suckers are brownish or brassy colored with clear fins, except for a dark blotch in the caudal fin (Etnier & Starnes 1993).

Nuptial body coloration varies from simple intensification of normal life colors (e.g., *Cycleptus* spp., some *Moxostoma* spp.) to the development of black or reddish lateral bands (e.g., the genera *Catostomus*, *Chasmistes*, *Thoburnia*, *Xyrauchen*; Etnier & Starnes 1993; Jenkins & Burkhead 1994; Moyle 2002). Some species (e.g., genera *Deltistes* and *Hypentelium*) do not develop nuptial coloration (Etnier & Starnes 1993; Jenkins & Burkhead 1994; Moyle 2002).

Catostomids develop distinctive patterns of breeding tubercles, also called pearl or contact organs that are keratonized epidermal structures that function to facilitate contact between spawning individuals (Fig. 13.18). The pattern of breeding tubercles across the body and the extent of their development have been of longstanding interest to naturalists and ichthyologists. Breeding tubercles of catostomids were mentioned by European naturalists as early as 1557 (Wiley & Collette 1970), and these structures were apparently mentioned in ancient Chinese documents (Wiley & Collette 1970 citing Kimura & Tao 1937). Some early works describing breeding tubercles in Suckers include Forbes and Richardson (1909); Fowler (1912), who described and illustrated tubercles on seven Suckers from eastern North America; Reighard (1920); Hubbs (1930); and Branson (1962). Tuberculation patterns are described for every genus in the family in North America (Huntsman 1967; Jenkins 1970; Wiley & Collette 1970; Madsen 1971; Morris & Burr 1982). Tubercle patterns vary a great deal in Suckers (Figs. 13.18 and 13.19); in fact, there is so much variation that Branson (1962) proposed a hypothesis on the evolution of tubercle patterns in catostomids. Wiley & Collette (1970) provided a comprehensive review of the early literature on breeding tubercles in catostomids, as well as other fishes, and presented information on their structure, function, and evolution.

Males of all species develop tubercles about the head, body, and fins. Tuberculation patterns range from small, fine tubercles covering the entire body (or portions of it) and fins (e.g., genera *Deltistes*; *Cycleptus*; *Ictiobus*; Fig. 13.18b) to the large snout tubercles developed by *Erimyzon* spp. (Fig 13.19). The morphology of these two types of tubercles is quite different. Tubercles on the body and fins of Golden Redhorse (*Moxostoma erythrurum*) are composed of "mounds of cells formed by epithelial hypertrophy and hyperplasia with keratinization of the tissue" (Wiley & Collette 1970:183). In contrast, the large snout tubercles on male *Erimyzon* are a "solid keratinized cone supported by vascularized hypertrophied epithelium" (Wiley & Collette 1970:183).

Internal Anatomy

Suckers have a physostomus swim bladder (i.e., a duct connects the swim bladder with the gut), like other Cypriniformes. Nelson (1961) compared swim bladder morphology in 52 species of catostomids. Hubbs (1930) used the number of chambers in the swim bladder as a main character in his taxonomic key to catostomid genera from eastern North America. The swim bladder in catostomids consists of two to four chambers. Genera with species having a two-chambered swim bladder include *Carpiodes*, *Catostomus*, *Cycleptus*, *Deltistes*, *Erimyzon*, *Hypentelium*, *Ictiobus*, *Minytrema*, *Thoburnia*, and *Xyrauchen*. Older literature (e.g., Hubbs 1930) reports the occasional presence of a third chamber in *Minytrema*; this was disputed by Nelson (1961), who did not find any indication of a third, posterior chamber in his survey of swim bladder morphology. In addition, the same literature reports the swim bladder of *Thoburnia* as being obsolete or absent. This absence can be attributed to the overall reduced size of the swim bladder, and to the fact that it is often obscured by being embedded in the retroperitoneal tissue in the anterodorsal body cavity (Nelson 1961). Three-chambered swim bladders occur in *Moxostoma*, except in the Bigeye Jumprock, which has either three or four chambers; when present, the fourth chamber is small and round (Jenkins & Burkhead 1994).

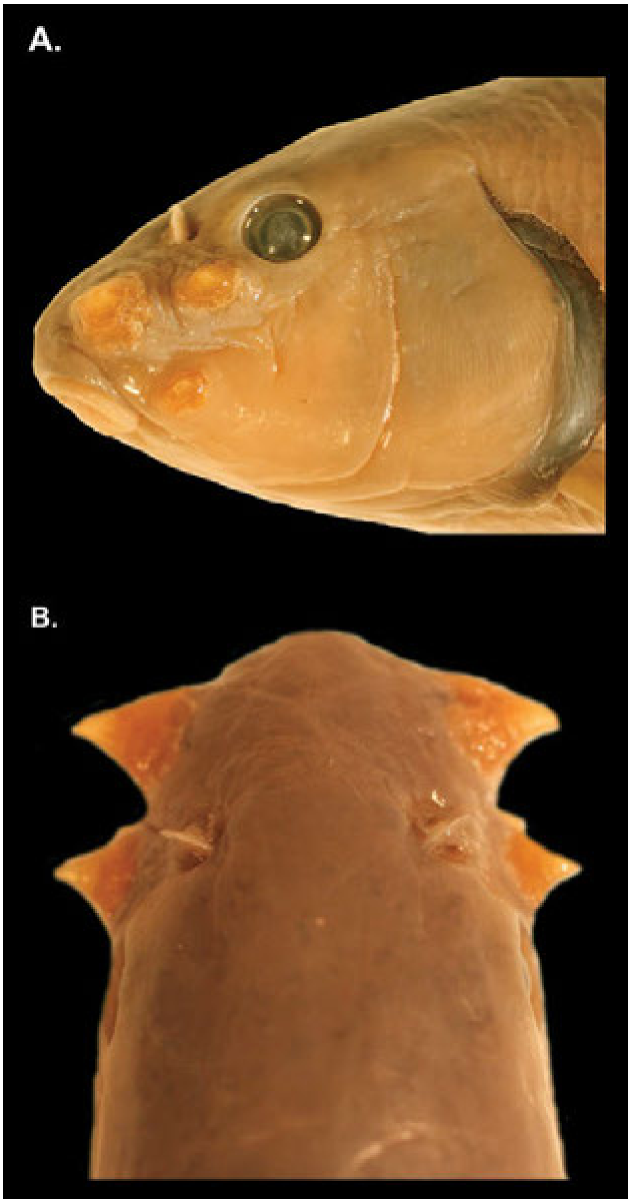


Figure 13.19. (A) Lateral and (B) dorsal views of breeding tubercles on the Creek Chubsucker, *Erimyzon oblongus* (UAIC 4383.08, male, 154 mm SL) (photograph by ®2010, P. M. Harris).

Osteology

Osteological characters of catostomids were used in a number of comparative studies with the primary goal of inferring evolutionary relationships within Catostomidae and among ostariophysans. Edwards (1926) illustrated the skull and associated muscles and ligaments in his examination of mechanisms of jaw protrusion in catostomids (see following subsection). Gregory (1933) also discussed jaw protrusion and illustrated the skull of

Carpiodes. Ramaswami (1957) illustrated the osteocranium and Weberian apparatus of *Catostomus commersonii* and *Myxocyprinus*; he also discussed seven osteological characters that he considered diagnostic of Catostomidae relative to other cypriniform fishes (see phylogenetic relationships section). Weisel (1960) provided a detailed description of the osteocranium and associated myology of the Largescale Sucker (*Catostomus macrocheilus*). Others described and illustrated the otoliths (Adams 1940), opercular series (Nelson 1949), Weberian apparatus (Nelson 1948; Robins & Raney 1956; Bailey 1959b; Cook 2001; Bird & Hernandez 2007), pharyngeal bones and teeth (Eastman 1977; Engeman et al. 2009), pectoral anatomy (Brousseau 1976), pectoral fin rays (Lundberg & Marsh 1976), and caudal skeleton (Eastman 1980). G. R. Smith (1992) used osteological and other characters to examine phylogenetic relationships among the Catostomidae; he provided illustrations or photographs and character state descriptions for several of these characters.

Functional Morphology of Feeding

Like other teleosts, Suckers can protrude their mouths and lips while feeding. In general, the same muscles and bones are involved in opening and closing the mouth (with the exception of *M. lacerum*, Jenkins 1994). Several characteristics of the bones, muscles, and ligaments of the mouth, however, allow for greater protrusibility than in other cypriniform fishes (described and illustrated in Edwards 1926 and Weisel 1960, and summarized here). First, the premaxillae are loosely attached to the preethmoid via the premaxillary spine and associated ligament. This loose attachment allows for greater rotation and protrusibility when the mouth is open. The extent of mouth protrusion corresponds with the lengths of the premaxillary spine and ligament. In addition, the premaxillae are not attached to the palatines via a ligament, allowing for increased freedom of movement. Second, a cartilaginous rod connects the maxillae with the vomer, creating a moving joint that allows for greater upper jaw movement. Third, the ascending process of the dentary is anterior in position. As the geniohyoideus and sternohyoideus muscles contract, this ascending process moves forward and downward. The ends of the premaxillae are attached to the ends of the maxillae by a ligament that, in turn, is attached to the ascending process of the dentary. Thus, this arrangement has the effect of pulling the premaxillae downward when the dentary is depressed. The overall result is the greater protrusibility of the mouth in catostomids, relative to that of cyprinids.

Manipulation and processing of food items is done by the pharyngeal bones and teeth. The pharyngeal bones are actually greatly enlarged ceratobranchials of the fifth arch (Weisel 1960; Eastman 1977). The pharyngeal teeth are composed of modified dentin (Peyer 1968), the compound that substitutes for enamel in fish teeth (Eastman 1977). Catostomids have a single row of ≥10 teeth; cyprinids have 1–3 rows of pharyngeal teeth with ≤5 teeth/row. Pharyngeal teeth are replaced throughout life. The number of pharyngeal teeth varies considerably among Suckers and is a function of tooth size and feeding ecology (Eastman 1977). Mollusk- and crustacean-eating species (e.g., Copper Redhorse, *Moxostoma hubbsi*, and River Redhorse, *Moxostoma carinatum*) have relatively few large, molariform teeth (20–22 and 35–41, respectively). In contrast species that feed on smaller-grained food items such as small crustaceans, insects, and algae, tend to have small, numerous teeth (e.g., carpsuckers, *Carpiodes* spp., or buffalofishes, *Ictiobus* spp., ≥175 teeth, Eastman 1977). In addition to large, molariform teeth, *M. hubbsi* and *M. carinatum* have large chewing pads associated with the basioccipital bone to aid in crushing mollusks. These pads are crescent shaped so that all the pharyngeal teeth occlude with the pad (Eastman 1977). Eastman (1977) provided a general survey of catostomid pharyngeal bones and teeth, including illustrations and a taxonomic key based on these elements.

Food particle selection and retention is accomplished, in part, by the palatal organ, which is a thick, muscular pad in the anterior roof of the pharynx (Eastman 1977; Callan & Sanderson 2003). The surface of the palatal organ is covered with taste buds, the number of which varies from about 50 (*M. carinatum*) to >130/cm^2 (*Carpiodes velifer*, Eastman 1977). The palatal organ of catostomids contains more striated muscle than that found in cyprinid palatal organs, which consist primarily of adipose tissue (Eastman 1977). Particle selection and retention is probably accomplished by muscular expansion of all, or part, of the palatal organ following stimulation of the taste buds, which results in food particles being held against the pharyngeal arches while other particles are expelled (Sibbing et al. 1986; Sibbing 1988). To our knowledge, no thorough, systematic review of the palatal organ in Suckers is available, and such a review is definitely needed to further understand the functional morphology of feeding in these fishes.

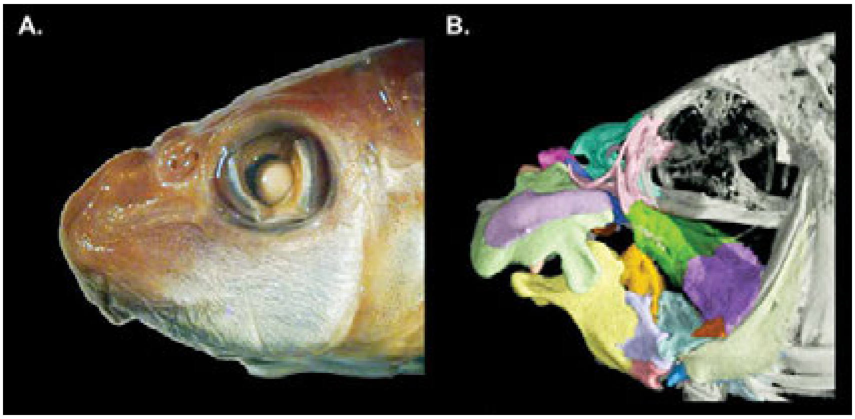


Figure 13.20. (A) Head of Harelip Sucker, *Moxostoma lacerum* (UMMZ 177435, 117 mm SL), right lateral view, image reversed. (B) Computer-generated x-ray tomographic image of lateral view of left side of head with individual bones color-coded. See Fink & Humphries (2010) for bone identifications (figure modified from Fink & Humphries 2010 and used with permission of the American Society of Ichthyologists and Herpetologists, copyright 2010). UMMZ = University of Michigan Museum of Zoology.

In an excellent example of the application of new technologies for study of functional morphology, Fink & Humphries (2010) used high-resolution x-ray computed tomography to examine the cranial and oral morphology of *M. lacerum* (Fig. 13.20). Harelip Suckers apparently fed on snails, based on the occurrence of snail operculi in stomachs of specimens examined (although snail shells were absent, Jenkins 1970, 1994). This diet is somewhat at odds with the morphology of the fifth ceratobranchial bone (pharyngeal tooth-bearing arch), which is not robust enough to crush snail shells. In addition, the pharyngeal teeth are slender (Fink & Humphries 2010:fig. 8), rather than molariform, as found in other snail- or crustacean-eating species (e.g., *M. carinatum* or *M. hubbsi*; Jenkins 1970; Eastman 1977). Also, *M. lacerum* possesses a bony shelf associated with the symphysis of the dentary (lower jaw) that is covered by a pad of keratinized tissue. Apparently, *M. lacerum* could manipulate snail shells so that it extracted the bodies while expelling the shells (Fink & Humphries 2010). Sadly, such speculation can never be tested because the Harelip Sucker is extinct, being last collected in 1893 (Jenkins & Burkhead 1994).

Intraspecific Variation

Species of Suckers often display a great deal of morphological variation across their respective distributions, particularly in western North American species of *Catostomus*. This variation led to the recognition of a number of subspecies by ichthyologists working in this region during the early 20th century. Given the extensive distributions of some species, attempts to comprehensively examine geographic intraspecific variation are limited. Studies of *Catostomus* (Smith 1966; Smith et al. 1983), *Cycleptus* (Burr & Mayden 1999), and *Moxostoma* (Robins & Raney 1956, 1957; Jenkins 1970) are notable exceptions. Other studies on morphological variation in catostomids were prompted by concerns over hybridization (e.g., Quist et al. 2009), especially between the lake Suckers (*Chasmistes* and *Deltistes*) and *Catostomus* (Cook 2001; Markle et al. 2005).

GENETICS

Karyology

Catostomids are allotetraploids and have a zygotic chromosome number of 100, about twice that of most diploid cypriniform fishes (Uyeno & Smith 1972). Based on fossil evidence and lack of multivalents in the meiotic spreads of *Erimyzon*, a single hybridization event 50 mya is postulated to account for the tetraploid catostomid karyotype (Uyeno & Smith 1972).

Electrophoretic studies of isozyme activities and mobilities are consistent with a rapid transition to disomic inheritance of most genes, enabling fixation and sequence divergence of duplicate genes (Ferris 1984). None of 20 catostomid isozyme loci showed evidence supporting tetrasomic inheritance (Allendorf 1975). In addition, isozymes of duplicate genes have different electrophoretic mobilities (Ferris & Whitt 1978), indicating sequence divergence.

Gene Silencing and Duplicate Gene Expression

Gene silencing is a prevalent phenomenon in catostomid evolution. Catostomids express 35–65% of their loci in duplicate, averaging 50% retention of ancestral duplicate gene expression with the remaining loci fixed for a null allele. Morphologically primitive species tend to express a greater proportion of their loci in duplicate with respect to more derived species (Ferris 1984).

Relative duplicate gene expression varies among and within tissues at different stages of development (Ferris 1984). Duplicate isozymes of lactate dehydrogenase B (LDH-B) and glucosephosphate isomerase B (GPI-B) are expressed in almost equal amounts in the embryos of Lake Chubsuckers, *Erimyzon sucetta*. LDH-B duplicate isozymes, however, are not expressed equally in adults, and only one isozyme of GPI-B is expressed in adult muscle (Shaklee et al. 1974). Two isozymes of creatine kinase B (CK-B) are expressed in the brain, but only one locus is expressed in the heart tissue of most catostomids (Ferris & Whitt 1979).

Duplicate gene expression of glucosephosphate isomerase in *Moxostoma* may provide evidence of reactivation of a silenced locus (Buth 1982). The Greater Jumprock (*Moxostoma lachneri*) expresses two GPI-A and two GPI-B loci. Other species of *Moxostoma* retain duplicate expression of GPI-A but express only a single GPI-B locus (Buth 1982). A parsimony analysis of gene-silencing events provided evidence of reactivation of a locus in *Minytrema melanops* (Ferris & Whitt 1978).

Regulatory mutations may play an important role in relative duplicate gene expression in catostomids (Ferris 1984). The less anodally migrating isozyme of LDH-B is less active as a result of regulatory control that reduces the message (Lim & Bailey 1977). Also, the less negative, acidic isozymes have weaker expression than duplicates with a greater net charge (Ferris & Whitt 1979). Natural selection may favor regulatory mutations that reduce relative expression of less stable, acidic isozymes (Ferris 1984).

Instances of duplicate gene silencing are used as phylogenetic characters in estimating relationships among catostomids (Ferris & Whitt 1977, 1978; Buth 1978, 1979). Ferris & Whitt (1978) examined duplicate gene expression in representative species of most North American genera. Duplicate gene expression characters also were used to infer phylogenies in Moxostomatini (Buth 1979b), in western North American Catostomini (Crabtree & Buth 1981, 1987), and in *Myxocyprinus asiaticus* (Tsoi et al. 1989). Buth et al. (1992) used duplicate gene expression and allozyme divergence as species-specific characters to investigate suspected hybridization of the Tahoe Sucker (*Catostomus tahoensis*) and Cui-ui (*Chasmistes cujus*) in Pyramid Lake, Nevada.

Genetic Variability

Catostomids have an average per-locus heterozygosity of 5% (Ferris & Whitt 1980); loci that retain duplicate expression have a higher average heterozygosity (7.6%) than loci that have been silenced (4.3%). Mean per-locus heterozygosity also differs among genera and species. The morphologically primitive genera *Ictiobus* and *Carpiodes* have an average heterozygosity of 9.2% (Ferris & Whitt 1980), but the genera *Catostomus*, *Hypentelium*, and *Moxostoma* typically have average heterozygosities of about 3% (Ferris 1984). But, this pattern does not always hold; the genus *Cycleptus* has low average heterozygosity, and the Shorthead Redhorse (*Moxostoma macrolepidotum*) has an average heterozygosity of 10% (Ferris 1984).

Hybridization and Introgression

Hybridization in nature among species and genera within Catostomidae is documented extensively (e.g., Hubbs et al. 1943; Hubbs & Miller 1953; Dauble & Buschbom 1981; Scribner et al. 2000). Hybridization is relatively frequent within the tribe Catostomini (Hubbs et al. 1943) and is documented within *Ictiobus* (Johnson & Minckley 1969) but is apparently less frequent among species of *Moxostoma*. Nine interspecific combinations of naturally occurring hybrids are known within *Catostomus* (Hubbs et al. 1943), and intergeneric hybrids between *Xyrauchen* and *Catostomus* (Hubbs & Miller 1953; Buth et al. 1987) and *Chasmistes* and *Catostomus* (Tranah & May 2006) are also known. Environmental disturbances may be associated with increased rates of hybridization (Nelson 1974), and the effect of artificial impoundment of waterways on hybridization rates among catostomids is an issue of considerable importance in their conservation.

Hybridization and introgression can result in a bewildering array of intra- and interspecific morphological variation (Markle et al. 2005), often obscuring taxonomic identities and phylogenetic relationships. These difficulties are particularly apparent in the evaluation of relationships among sympatric Suckers from western North America. The endangered, endemic June Sucker (*Chasmistes liorus*) and the wider-ranging Utah Sucker (*Catostomus ardens*) inhabit Utah Lake, Utah. The Suckers of Utah Lake display a gradient of morphologies from individuals apparently adapted to the benthic feeding characteristic of *C. ardens* to mid-level planktivorous individuals that display characteristic *C. liorus* morphology to a spectrum of intermediate forms (Mock et al. 2006). Based on the morphology of contemporary and museum specimens, a severe drought in the 1930s was postulated to cause extensive hybridization between *C. ardens* and *C. liorus*, resulting in the formation of the hybrid lineage *C. liorus mictus* and the subsequent extinction of *C. liorus* (Miller & Smith 1981). Cook (2001), however, asserted morphological evidence is insufficient to support a hypothesis of hybridization between these lineages. Similarly, analyses of mitochondrial DNA sequences and amplified fragment length polymorphism data do not support the hypothesis of hybridization between these lineages in Utah Lake (Mock et al. 2006). Fairly recent ecological selection may have contributed to the divergent morphologies of Suckers in Utah Lake (Cook 2001; Mock et al. 2006).

The Suckers of the Klamath Basin, Oregon and California, present another example of an apparent disconnect between the phylogenetic signals provided by morphology and genetics that may be the result of hybridization and introgression (Markle et al. 2005). The Klamath Basin is inhabited by three genera of catostomids represented by four native species with a wide range of morphological characteristics. The endangered Shortnose Sucker (*Chasmistes brevirostris*) and Lost River Sucker (*Deltistes luxatus*) may be introgressed and may continue to hybridize with the non-imperiled Klamath Largescale Sucker (*Catostomus snyderi*) and Klamath Smallscale Sucker (*Catostomus rimiculus*, Miller & Smith 1981). Using a combination of amplified fragment length polymorphism and single strand conformation polymorphism techniques, four of these species and their hybrids were distinguished, but little genetic variation was present among these lineages (Tranah et al. 2003).

The Zuni Bluehead Sucker (*Catostomus dicobolus yarrowi*) displays morphological characters similar to those of the Bluehead Sucker (*C. discobolus*) with respect to the number of gill rakers and similar to those of the Rio Grande Sucker (*Catostomus plebeius*) in numbers of vertebrae and dorsal fin rays, jaw morphology, and pigmentation (Smith 1966). Based on morphological data, Smith (1966) hypothesized that *C. d. yarrowi* is an intergrade resulting from a Late Pleistocene stream capture. The capture led to introgression of *C. plebeius* characters into the genome of *C. discobolus* populations inhabiting the headwaters of the Little Colorado River drainage, New Mexico and Arizona. Meristic and morphometric data and variation in 35 allozyme loci were cited as supporting the hypothesis of stream capture and introgressive origin of *C. d. yarrowi* (Smith et al. 1983). An expanded reexamination of allozyme data revealed evidence of introgression of *C. plebeius* into *C. d. yarrowi* in a single creek in New Mexico but refuted the hypothesis that *C. d. yarrowi* originated from introgressive hybridization (Crabtree & Buth 1987).

Hybridization between *Catostomus commersonii* and *C. macrocheilus* is fairly common in three drainages in British Columbia (J. S. Nelson 1968). Nine of 11 lakes examined were occupied by putative F_1 hybrids comprising an average of 7% of the individuals examined. Hybridization between the two species does not result in increased embryo mortality, and F_1 hybrids are fertile, suggesting the absence of post-reproductive isolating mechanisms. Despite the apparent fertility of hybrids, all hybrid specimens examined were presumed to be F_1 progeny (J. S. Nelson 1968). To our knowledge, no one has looked for successful reproduction among the F_1 progeny or introgression of these hybrids back into the parental genomes. Ethological isolation is probably the most important mechanism preventing initial hybridization with *C. commersonii* spawning over shallow gravel substrates and *C. macrocheilus* spawning over deeper, sandier substrates (J. S. Nelson 1968).

Morphologically divergent species within *Catostomus* may hybridize in areas of sympatry. The Sonora Sucker (*Catostomus insignis*) and Desert Sucker (*Catostomus clarki*) are broadly sympatric and hybridize throughout a wide region (Clarkson & Minckley 1988). *Catostomus clarki* is morphologically adapted for specialized feeding by scraping organic material from solid substrates, but *C. insignis* is a generalized carnivore (Schreiber & Minckley 1982). Putative F_1 hybrids of the two species are intermediate with respect to characteristic morphological traits but display wide variation in feeding behavior, spanning the feeding strategies used by the parental species (Clarkson & Minckley 1988).

Anthropogenic environmental disturbances (e.g., dams, species introductions) are associated with the occurrence and frequency of hybridization in Suckers (Cooke et al. 2005). Based on morphological characters, hybridization between *Ictiobus bubalus* and *I. niger* (Heard 1958) and between *I. cyprinellus* and *I. bubalus* (Johnson & Minckley 1969) is documented in reservoirs. *Catostomus commersonii* and *C. catostomus* rarely hybridize under natural conditions (Nelson 1973). They did so in the upper Kananaskis reservoir, Alberta, and the hybridization is associated with introduction of both species to the reservoir, environmental disturbance related to water level fluctuations caused by hydroelectric generation, and high numbers of

C. catostomus relative to *C. commersonii* (Nelson 1973). In contrast, frequency of hybridization between *C. commersonii* and *C. macrocheilus* in the Williston reservoir, British Columbia, following impoundment of the Peace River was not higher than that of populations inhabiting relatively undisturbed habitats (Nelson 1974).

Molecular Markers

A number of biochemical and molecular markers are used in the identification and analysis of genetic variation within and among populations of catostomids. Analyses of mitochondrial DNA sequences, microsatellite DNA markers, amplified fragment length polymorphisms (AFLP), and allozyme data were used to examine taxonomic identity (Tranah et al. 2003; Mock et al. 2006; Tranah & May 2006), potential inbreeding due to small effective population sizes (Lippe et al. 2006), interspecific or intergeneric hybridization (Tranah & May 2006), identification of early life history stages (Wirgin et al. 2004), assessment of genetic variation before captive propagation (Wirgin et al. 2001), and post-propagation population monitoring (Dowling et al. 2005).

Microsatellite DNA primers are developed for a variety of catostomid taxa, including the genera *Cycleptus* (Bessert et al. 2007), *Catostomus*, *Chasmistes*, *Deltistes* (Tranah et al. 2001b; Cardall et al. 2007), and *Moxostoma* (Lippe et al. 2004). These studies include cross-species amplification profiles for the microsatellite DNA primers, indicating their probable utility in other catostomid taxa. Although some initial cost is associated with their development, microsatellite DNA markers have the potential to address a number of important questions associated with conservation, especially estimates of intra- and interpopulation genetic diversity, gene flow, and the size of the reproductive population. For example, analysis of 21 polymorphic microsatellite loci of *Moxostoma hubbsi* indicated that populations retained much of their diversity in spite of recent severe population declines and fragmentation throughout the limited range of this imperiled species (Lippe et al. 2006). Although long generation time may have slowed the loss of genetic diversity, simulations indicated that the effective population size of *M. hubbsi* must remain >400 individuals in order to preserve 90% of the species' genetic diversity over the next century.

One of the difficulties frequently encountered by researchers studying the genetics of polyploid organisms like Suckers is the co-amplification of paralogous loci when using nuclear markers such as microsatellite DNA. Bessert et al. (2007) used cloning and sequencing to isolate 11 microsatellite DNA loci from their paralogs in *Cycleptus elongatus*. An alternative approach using AFLP and single strand conformation polymorphism techniques was used in the development of three co-dominant markers for the analyses of genetic identity among Suckers of the Klamath Basin (Tranah et al. 2003). One of several factors threatening endangered *C. brevirostris* and *D. luxatus* is the progressive loss of genetic identity through introgression or hybridization with sympatric, non-imperiled *Catostomus snyderi* and *C. rimiculus* (Markle et al. 2005). Co-dominant markers specific to these two species (Tranah et al. 2003) are useful in the identification of hybrid individuals and monitoring of introgression among Suckers of the Klamath Basin.

Geographic Genetic Variation

Studies of geographic genetic variation in catostomids are limited. Most allozyme studies of geographic variation concentrated on *Catostomus* (Buth & Crabtree 1982; Ferris et al. 1982; Buth et al. 1987) and *Cycleptus* (Buth & Mayden 2001). These studies (Ferris et al. 1982; Buth et al. 1987; Buth & Mayden 2001) revealed significant geographic structuring of populations, although this is not always the case (e.g., Buth & Crabtree 1982).

Modern molecular techniques have added new insights into our understanding of geographic genetic variation in catostomids, especially by revealing previously unrecognized clades and the influence of historic factors in shaping current lineages (Wirgin et al. 2001; Berendzen et al. 2003; Mock et al. 2006). Only two papers on catostomids are published to date explicitly using phylogeography in the title or abstract. Berendzen et al. (2003) used mitochondrial DNA sequences to examine phylogeographic patterns in *Hypentelium*. Their results demonstrated concordance between mitochondrial lineages within *Hypentelium nigricans* (Northern Hog Sucker) and paleohydrological drainage patterns in eastern North America. Using a combination of mitochondrial DNA sequences and microsatellite DNA markers, McPhee et al. (2008) also reported phylogeographic patterns structured by drainage for the Rio Grande Sucker in New Mexico.

PHYSIOLOGY

Environmental pH Tolerances

The physiological response of catostomids to extreme environmental acidity or alkalinity is documented in several species. Increased anthropogenic nutrient inputs into upper Klamath Lake, south-central Oregon, result in summer and autumn blooms of the blue-green algae, *Aphanizomenon flos-aquae*, leading to increases in ambient pH values (pH 9.5–10.5) that last several weeks (Falter & Cech 1991). In controlled experiments, *Catostomus snyderi* and *Chasmistes brevirostris* displayed sustained loss of equilibrium at pH 10.73 and 9.55, respectively. The pH maximum of *C. brevirostris* is significantly lower than for sympatric species *C. snyderi* and the Tui Chub (*Siphateles bicolor*) and is not correlated significantly with body mass. The comparatively low critical pH maximum of *C. brevirostris* makes it particularly susceptible to environmental alkalinity during seasonal phytoplankton blooms. Increased ambient pH may be an important factor in *C. brevirostris* population declines in upper Klamath Lake (Falter & Cech 1991).

Physiological stress resulting from exposure to low environmental pH significantly affects ionoregulation in *Catostomus commersonii* (Fraser & Harvey 1984; Hobe et al. 1984; Hobe & McMahon 1988). Survival in acidic environments is related largely to the ability to prevent loss of sodium ions (Fraser & Harvey 1984). Rapid branchial loss of sodium ions in acidic water (pH 4.0–4.5) leads to decreased plasma osmotic pressure, resulting in decreased extracellular fluid volume and increases in intracellular fluid pressure, hematocrit, hemoglobin concentration, red blood cells, blood viscosity, and blood pressure. Loss of sodium ions in acidic ecosystems is ameliorated by high ambient concentrations of calcium ions, such that low ambient pH is most deleterious to fish populations in soft-water environments (Fraser & Harvey 1984). *Catostomus commersonii* exposed to acidic soft water exhibit rapid, shallow ventilatory pumping and secrete white mucus that covers the gills and skin, partially reducing branchial ion efflux and gas exchange (Hobe et al. 1984). Acute exposure of *C. commersonii* to acidic soft water at pH 4.3 results in rapid net influx of protons; whole-body losses of sodium, chloride, calcium, and potassium ions; plasma acidosis from altered respiratory and metabolic function; reduced plasma oxygen partial pressure; increased plasma carbon dioxide partial pressure; increased blood lactate; and increased hemoconcentration (Hobe et al. 1984). Exposure of *C. commersonii* to acidic soft water at pH 4 for 48 h results in complete mortality (Fraser & Harvey 1984). During a fluctuating ambient pH regime consisting of alternating exposure to soft water at pH 4 and pH 7, the deleterious effects of acid exposure on *C. commersonii* are not ameliorated by periods of exposure to neutral ambient pH. Fluctuating ambient pH may be more detrimental to *C. commersonii* inhabiting soft-water ecosystems than gradual, continued exposure to low ambient pH (Hobe & McMahon 1988).

Juvenile Robust Redhorse (*Moxostoma robustum*) exhibit a relatively broad range of pH tolerance in laboratory trials. Juveniles exhibited no mortality over a 96-h period when exposed to soft water with pH values ranging from 4.6 to 9.0. Complete mortality of juvenile *M. robustum* resulted from exposure to extremely alkaline soft water within the first 3 h at pH ≥10.5, within 55 h at pH 9.9, and within 70 h at pH 9.5. When exposed to extremely low ambient pH, juveniles exhibited complete mortality within 11 h at pH 4.0 and 90% mortality over a 96-h exposure at pH 4.3 (Walsh et al. 1998).

Low ambient pH values significantly affect the reproductive life history of *C. commersonii*. Maturation occurs later and at larger body sizes in *C. commersonii* from acidic lakes in Ontario with ambient pH ranging from 4.9 to 5.6 than in fish from two lakes with pH values of 6.30 and 6.35 (Trippel & Harvey 1987ab). In females and males the reproductive lifespan of *C. commersonii* is longer in circumneutral lakes than in lakes with low ambient pH. In contrast to adults in circumneutral lakes, individuals from acidic lakes exhibit increased mortality rates with the onset of sexual maturity. Later onset of sexual maturity and greater reproductive output for a shorter duration before high post-spawning mortality may represent an adaptive life history strategy for *C. commersonii* under the physiologically stressful conditions of low ambient pH (Trippel & Harvey 1987ab).

Thermal Biology and Metabolism

Physiological temperature tolerances and the effects of ambient temperature on respiratory metabolism are known for adults and juveniles in several species of catostomids. In *C. commersonii* from headwater streams in Missouri, the critical maximum temperature (loss of equilibrium) was 34.9°C, and minimum dissolved oxygen concentration at cessation of opercular movements was 0.98 mg/l (Smale & Rabeni 1995). The hyperthermia tolerance of *C. commersonii* was lower and the hypoxia tolerance intermediate relative to other fishes collected from the same headwater streams.

Critical thermal maxima in adults are known for some species in almost all catostomid genera (Tables 13.2–13.13); the range of critical temperatures for these species is about 30–39°C. To our knowledge, however, the interaction

Table 13.2. Life history traits of *Carpiodes*.

Life History Trait	Description	References
Strictly freshwater (ppt)	Yes, 0.9–5.8[1]	Echelle et al. (1972)
Critical thermal maxima	37–39°C	Spotila et al. (1979), Mundahl (1990)
Maximum size recorded in length and weight	500 mm TL; 5.45 kg	Trautman (1981)
Maximum age	10–13 years	Vanicek (1961), Woodward & Wissing (1976)
Age and size at first reproduction	2–3 years; 200–250 mm TL	Trautman (1981), Jester (1972)
Iteroparous or semelparous	Iteroparous	
Fecundity estimates (ovarian counts)	5,000–200,000	Behmer (1969), Boschung & Mayden (2004)
Mature egg diameter	1.7–2.1 mm	Behmer (1969), Yeager (1980)
Egg deposition sites	Firm gravel bottom, free of vegetation; spawning may occur at night or afternoon	Bucholz (1957), Walburg & Nelson (1966), Jester (1972)
Range of nesting dates and temperatures	April–September; >31°C	Woodward & Wissing (1976)
Habitat of spawning sites; average water depth	Slow sections and overflow pools of small streams; 0.3–1.0 m deep	Bucholz (1957), Walburg & Nelson (1966)
Incubation period; larval type at hatching	5–13 days at 15–27°C; yolk-sac larva	Kay et al. (1994)
Mean size at hatching and swim-up	5–6 mm TL	Yeager (1980)
Parental care	No	
Major dietary items (adults)	Crustaceans, chironomids, diatoms, filamentous algae, duckweed	Eastman (1977)
General year-round habitat	Main channels of larger streams and rivers, over sand and gravel, free of vegetation	Trautman (1981), Boschung & Mayden (2004)
Migratory or diadromous	Spawning migrations	Curry & Spacie (1984)
Imperilment status	*C. velifer* in decline	Boschung & Mayden (2004)

[1] Salinity at collection locality.

between critical thermal maxima and critical dissolved oxygen minima is known only for two species of Suckers inhabiting the Klamath Basin. *Chasmistes brevirostris* and *C. snyderi* have critical thermal maxima between 32 and 33°C (Castleberry & Cech 1992). Both species also have comparable critical dissolved oxygen minima between 11.8 and 12.7 torr (Castleberry & Cech 1992). Because dissolved oxygen levels are often lowest below the thermocline in lakes during summer, benthically oriented species such as *C. brevirostris* and *C. snyderi* are particularly susceptible to low dissolved oxygen levels in upper Klamath Lake where concentrations can be ≤5 torr (Scoppettone et al. 1986).

Reduced water temperatures from hypolimnetic dam discharges reduce hatching success, development rate, and oxygen consumption of *Xyrauchen texanus* (Bozek et al. 1990). In laboratory experiments, no eggs incubated at 8°C successfully hatched (Marsh 1985; Bozek et al. 1990). Egg mortality, occurring largely at pre-morula stages of development, was higher at 10°C than at 15 or 20°C (Bozek et al. 1990). Development rate and oxygen consumption of *X. texanus* were related positively to temperature.

Upper and lower critical thermal maxima of 1-, 2-, and 3-month-old juvenile *M. robustum* were determined in experiments involving sudden, acute exposure to physiologically stressful conditions. Lower critical thermal maxima were influenced significantly by acclimation temperature and ranged from 5.3°C for 3-month-old juveniles (acclimated at 15°C) to 19.4°C for 2-month-old fish (acclimated at 30°C) (Walsh et al. 1998). Age did not significantly affect upper and lower critical thermal maxima within acclimation temperature groups. Average critical thermal maxima ranged from 34.9°C for fish acclimated at 20°C to 37.16°C for fish acclimated at 30°C. Juvenile *M. robustum* displayed increased rates of opercular ventilation at and near upper critical thermal maxima with fish acclimated at 20°C displaying higher ventilatory frequency than those acclimated at 30°C.

Lower temperatures significantly affect the cardiac output of *Catostomus macrocheilus*. The critical swimming

Table 13.3. Life history traits of *Catostomus*.

Life History Trait	**Description**	**References**
Strictly freshwater (ppt)	Yes, ≤13[1]	Reimers & Bond (1967), Moyle (2002)
Critical thermal maxima	32–35°C	Reutter & Herdendorf (1976), Castleberry & Cech (1992), Smale & Rabeni (1995)
Maximum size recorded in length and weight	800 mm TL; weight not given	Page & Burr (1991)
Maximum age	10–20+ years	Hauser (1969), Dauble (1986)
Age and size at first reproduction	2–3 years; 70–150 mm TL	Hauser (1969), Dauble (1986)
Iteroparous or semelparous	Iteroparous	Geen et al. (1966), Bailey (1969)
Fecundity estimates (ovarian counts)	2,000–140,000	Stewart (1926), Vessel & Eddy (1941)
Egg deposition sites	Small streams, shoals, or shorelines free from vegetation and silt, 10–150 cm	Bailey (1969), Curry & Spacey (1984)
Mature egg diameter	1.7–3.6 mm	Stewart (1926), Fish (1932), Fuiman & Witman (1979), Dauble (1986)
Range of nesting dates and temperatures	March–July; 10–15°C	Raney (1943), Dauble (1986)
Habitat of spawning sites; average water depth	Rocky areas of small streams or shorelines of lakes, twilight hours	Curry & Spacey (1984), Raney (1943)
Incubation period; larval type at hatching	4–15 days, 10–21°C; yolk-sac larva	Raney & Webster (1942), Long & Ballard (1976)
Mean size at hatching and swim-up	8–12 mm	Fuiman & Whitman (1979)
Parental care	None	
Major dietary items (adults)	Diatoms, dipteran larvae, mollusks, cladocerans, copepods, detritus, fish eggs	Dauble (1986)
General year-round habitat	Cool, well-oxygenated streams, rivers, and lakes	Page & Burr (1991)
Migratory or diadromous	Spawning migrations	Werner (1979), Dauble (1986)
Imperilment status	22 species Vulnerable, Threatened, or Endangered	Jelks et al. (2008)

[1] Salinity at collection locality.

speed, maximum cardiac output, and scope of cardiac output were significantly lower in swimming *C. macrocheilus* at 5°C relative to values at 10°C but were not different within the range of 10–16°C (Kolok et al. 1993). Cardiac and swimming performance of *C. macrocheilus* is significantly reduced at temperatures <10°C. At 16°C the majority of blood flow is directed to white muscle and the kidneys in resting *C. macrocheilus*. Blood flow to red muscle increases 60-fold in swimming fish relative to fish at rest at the same temperature (Kolok et al. 1993).

Egg survival, egg development rate, and larval size of *Chasmistes cujus* in the Truckee River, Nevada, are affected negatively by elevated water temperature. In a series of experiments using four fluctuating temperature regimes, survival of swim-up larvae was significantly lower at the highest temperature regime of 17.8–23.9°C but was not different among regimes of 8.9–15, 12.2–18.3, and 15.0–21.1°C (Scoppettone et al. 1983). Time to hatching and swim-up were inversely proportional to temperature. Average TL of larvae was greatest at the lowest temperature regime, and significantly decreased with increasing temperature. As a consequence, elevated springtime water temperatures in the Truckee River due to agricultural and municipal water use may adversely affect the reproductive success of *C. cujus* (Scoppettone et al. 1983).

Catostomus tahoensis inhabits lotic ecosystems where it is exposed to daily fluctuations in temperature and lentic ecosystems in which daily water temperatures are more constant (Vondracek et al. 1982). In cyclic and constant thermal regimes the oxygen consumption rate of *C. tahoensis* increased exponentially with increasing temperature from 8 to 18°C. From 8 to 13°C respiratory metabolic rate was similar for cyclic and constant temperature regimes. The rate of oxygen consumption at 18°C was significantly

Table 13.4. Life history traits of *Chasmistes*.

Life History Trait	Description	References
Strictly freshwater (ppt)	Yes, 5.5 (spawns <1.8)	Chatto (1979)
Critical thermal maxima	32.7°C	Castleberry & Cech (1992)
Maximum size recorded in length and weight	670 mm; weight not given	Snyder (1917)
Maximum age	44+ years	Belk (1998), Scoppettone et al. (2000)
Age and size at first reproduction	5–7 years; 440–490 mm	Belk (1998), Shirley (1983)
Iteroparous or semelparous	Iteroparous	La Rivers (1994)
Fecundity estimates (ovarian counts)	30,000–60,000	Coots (1965), Koch (1973), Sigler et al. (1985)
Mature egg diameter	2.0 mm	Koch (1973), Sigler et al. (1985)
Egg deposition sites	Swift streams and rivers with cobble gravel substrate	Snyder (1917)
Range of nesting dates and temperatures	April–May	Snyder (1917)
Habitat of spawning sites; average water depth	Shallow riffles and gravel runs	Snyder (1917)
Incubation period; larval type at hatching	9 days at 13°C; yolk-sac larva	Sigler et al. (1985)
Mean size at hatching and swim-up	6–7 mm, 12–14 mm	Koch (1976), Sigler et al. (1985)
Parental care	None	
Major dietary items (adults)	Cladocerans, copepods, filamentous algae	La Rivers (1994)
General year-round habitat	Pelagic and inshore benthic	La Rivers (1994), Sigler et al. (1985)
Migratory or diadromous	Spawning migrations	La Rivers (1994)
Imperilment status	All species federally Endangered	Jelks et al. (2008)

higher in *C. tahoensis* exposed to a cyclic thermal regime than in fish exposed to a constant regime. As a result of higher respiratory metabolic rates, stream-dwelling *C. tahoensis* may exhibit slower growth rates or increased food requirements in comparison to those inhabiting more thermally stable environments (Vondracek et al. 1982).

Physiological Effects of Saline Exposure

Catostomids are freshwater stenohaline fishes that rarely inhabit brackish or saline habitats (Tables 13.2–13.13). Possible exceptions are the Sacramento Sucker (*Catostomus occidentalis*) that occurs in Suisun Marsh, California, in water with salinities >13 ppt (Moyle 2002) and *C. macrocheilus* that is known from brackish areas in the lower Columbia River (Reimers & Bond 1967). Studies of salinity tolerances are available for the early life history stages of *Ictiobus* (Hollander & Avault 1975), juvenile *M. robustum* (Walsh et al. 1998), and adult *C. commersonii* (Wilkes & McMahon 1986a).

Eggs of *Ictiobus* are more tolerant of saline conditions (15 ppt) than any other early life history stage (Hollander & Avault 1975) due to the egg chorion acting as an osmotic barrier. As juveniles approach 1 year old, their salinity tolerance drops to 10 ppt (Hollander & Avault 1975).

Acute exposure of juvenile *M. robustum* to salinities ≥9 ppt results in 50% mortality within 53 h (Walsh et al. 1998); however, water alkalinity can ameliorate the effects of salinity. Juvenile *M. robustum* acclimated in soft water experienced complete mortality at 4–6 ppt, but fish acclimated in hard water survived to 12 ppt. In addition, body mass and salinity tolerance were related positively in experiments exposing laboratory-reared juveniles acclimated in hard water to chronic increases in salinity (Walsh et al. 1998).

Exposure of *C. commersonii* to a maximum sublethal salinity of 300 mosmol/liter has significant effects on plasma electrolyte regulation and acid-base status (Wilkes & McMahon 1986a). Stenohaline freshwater fishes cannot survive hypersaline conditions when plasma osmolality falls below ambient conditions. Salinity exposure resulted in increases in plasma concentrations of Na^+ and Cl^- with a greater increase in Cl^- concentration relative to Na^+ concentration, leading to a decrease in strong ion difference. At constant plasma carbon dioxide concentrations saline exposure resulted in decreases in plasma pH and bicarbonate concentration, but apparent proton load remained unchanged despite decreased plasma pH. Plasma acid-base status was determined by

Table 13.5. Life history traits of *Cycleptus*.

Life History Trait	**Description**	**References**
Strictly freshwater (ppt)	Yes	
Critical thermal maxima	Unknown	
Maximum size recorded in length and weight	930 mm TL; 11.3 kg	Rupprecht & Jahn (1980), Page & Burr (1991)
Maximum age	12 years observed, possibly up to 33 years	Peterson et al. (1999)
Age and size at first reproduction	Males, 3 years, 507 mm TL; females, 11 years, 554 mm TL	Rupprecht & Jahn (1980), Moss et al. (1983), Peterson et al. (1999)
Iteroparous or semelparous	Iteroparous	Moss et al. (1983), Mettee et al. (2003)
Fecundity estimates (ovarian counts)	100,000–200,000	Rupprecht & Jahn (1980)
Mature egg diameter	2.2 mm	Moss et al. (1983)
Egg deposition sites	Runs with cobble and gravel bottoms	Moss et al. (1983)
Range of nesting dates and temperatures	March–June; 15–23°C	Moss et al. (1983), Mettee et al. (2003)
Habitat of spawning sites; average water depth	Deep riffles with cobble and bedrock; 1–2 m	Moss et al. (1983)
Incubation period; larval type at hatching	6 days at 16.6–20°C; yolk-sac larva	Clay (1975)
Mean size at hatching and swim-up	6.4–8.7 mm	Semmens (1985), Yeager & Semmens (1987)
Parental care	None	
Major dietary items (adults)	Insect larvae and pupae: trichopterans, chironomids, coleopterans, and nematodes	Moss et al. (1983)
General year-round habitat	Deep (1–2 m) swift riffles and runs over firm substrate	Pflieger (1997), Moss et al. (1983), Mettee et al. (2003), Boschung & Mayden (2004)
Migratory or diadromous	Spawning migrations, with strong interannual spawning site fidelity	Pflieger (1997), Peterson et al. (2000), Mettee et al. (2003)
Imperilment status	Either Vulnerable or Threatened	Jelks et al. (2008)

the change in plasma strong ion difference in *C. commersonii* exposed to maximum sublethal salinity (Wilkes & McMahon 1986a).

The observed decrease in strong ion difference and plasma pH in *C. commersonii* exposed to maximum sublethal salinity largely results from transepithelial movement of sodium and chloride (Wilkes & McMahon 1986b). In control fish not exposed to saline water, transepithelial potential is negative in fish acclimated in soft water but positive in fish acclimated in hard water. In contrast, external calcium has less influence on transepithelial potential during saline exposure as evidenced by the fact that transepithelial potential remains positive in saline-stressed fish in both hard and soft water. Passive transepithelial movement of sodium outward and of chloride inward resulting from the prevailing transepithelial potential may account for the decrease in strong-ion difference and plasma pH during saline stress in *C. commersonii* (Wilkes and McMahon 1986b).

In vitro experiments involving blood from control fish approximating the decreased strong-ion difference and acidosis of *C. commersonii* exposed to maximum sublethal salinity show that these conditions result in reduced hemoglobin oxygen affinity (Walker et al. 1989). Nevertheless, blood collected from saline-exposed fish shows no significant decrease in hemoglobin oxygen affinity when compared to that of control fish. Hypersaline exposure results in reduced plasma pH, red blood cell pH, plasma total carbon dioxide, and erythrocyte nucleoside triphosphate and increased erythrocyte volume and plasma catecholamine. Increased plasma catecholamine concentration and decreased nucleoside triphosphate in red blood cells may compensate for acidosis-induced reduction in hemoglobin oxygen affinity in saline-stressed *C. commersonii* (Walker et al. 1989).

Table 13.6. Life history traits of *Deltistes*.

Life History Trait	Description	References
Strictly freshwater (ppt)	Yes	
Critical thermal maxima	Unknown	
Maximum size recorded in length and weight	1 m; 4.5 kg	Moyle (2002)
Maximum age	43 years	Scoppettone & Vinyard (1991)
Age and size at first reproduction	5–9 years; size not given	Buettner & Scoppettone (1990), Scoppettone & Vinyard (1991)
Iteroparous or semelparous	Iteroparous	Scoppettone & Vinyard (1991)
Fecundity estimates (ovarian counts)	101,000–235,000	Golden (1969), Andreasen (1975)
Egg deposition sites	Loose gravel	Scoppettone & Vinyard (1991)
Mature egg diameter	Unknown	
Range of nesting dates and temperatures	February–May; 4–15°C	Scoppettone & Vinyard (1991), Evans et al. (2009)
Habitat of spawning sites; average water depth	Rocky substrate; 28–128 cm, 0.01–0.8 m/s velocity,	Perkins & Scoppettone (1996)
Incubation period; larval type at hatching	Unknown	
Mean size at hatching and swim-up	Unknown	
Parental care	None	
Major dietary items (adults)	Detritus, invertebrates	Evans et al. (2009)
General year-round habitat	Open-water lacustrine	Moyle (2002)
Migratory or diadromous	Spawning migrations	Perkins & Scoppettone (1996)
Imperilment status	Endangered	Jelks et al. (2008), Evans et al. (2009)

Chemoreception

Like other members of Cypriniformes, catostomids display a behavioral alarm reaction when exposed to chemical substances released from the skin of injured cypriniform fishes (Doving et al. 2005). Though little research focused specifically on catostomids, threshold concentrations required to elicit an alarm reaction are known for *C. catostomus* and *C. macrocheilus* (Pfeiffer 1963). Since Karl von Frisch discovered the alarm reaction in minnows in 1938, the origin, chemical nature, and sensory basis for the alarm reaction have been investigated in depth in a variety of cypriniform fishes (Doving et al. 2005) and are putatively similar for catostomids.

The alarm substance, or Shreckstoff, is produced in secretory epidermal club cells. These cells lack a connection to the epidermal surface in fishes that produce an alarm substance (Doving et al. 2005). When club cells are ruptured by injury to the fish the alarm substance is released. Pterin-like proteins, hypoxanthine oxides, carbohydrates, and oligopeptides are all implicated in causing the alarm reaction in cypriniform fishes. Biochemical studies consistently identify a single, stable compound as the pheromone responsible for the fright reaction in cypriniform fishes, but behavioral studies demonstrate that the fright substance is ephemeral and largely species-specific, suggesting that several, unstable compounds may be involved in induction of the fright response (Doving et al. 2005).

The alarm pheromone is detected by the olfactory system (Doving et al. 2005). *C. catostomus* and *C. macrocheilus* each have a sensitivity threshold of 0.01 g/l of skin before an alarm reaction is elicited (Pfeiffer 1963). Coho Salmon (*Oncorhynchus kisutch*) display a distressed behavioral reaction to skin extracts from *C. macrocheilus*, possibly indicating a defensive toxic compound or another form of interspecific chemical-signaling substance present in the skin (Jobling 1995).

Vision

Catostomus commersonii is visually sensitive to ultraviolet light, like many other teleosts; however, the arrangement and histology of UV-sensitive cones in the retina of *C. commersonii* are unique among all other teleosts studied to date. Cyprinids and salmonids that are sensitive to UV also can discriminate the polarization of UV light. Polarization sensitivity in these fishes is

Table 13.7. Life history traits of *Erimyzon*.

Life History Trait	Description	References
Strictly freshwater (ppt)	Yes, 0–0.99[1]	Lorenz and Serafy (2006)
Critical thermal maxima	Unknown	
Maximum size recorded in length and weight	419 mm; weight not given	Carlander (1969)
Maximum age	5–6 years	Boschung & Mayden (2004)
Age and size at first reproduction	2 years; about 150 mm TL	Carnes (1958), Jenkins & Burkhead (1994), Boschung & Mayden (2004)
Iteroparous or semelparous	Iteroparous	Boschung & Mayden (2004)
Fecundity estimates (ovarian counts)	3,000–83,000	Cooper (1935), Carnes (1958)
Mature egg diameter	About 1.8–2.0 mm	Cooper (1935), Carnes (1958)
Egg deposition sites	Gravel in streams, vegetation in still water	Scott & Crossman (1973), Curry & Spacie (1984), Fuiman (1979)
Range of nesting dates and temperatures	March–June; 11–23°C	Cooper (1935), Jenkins & Burkhead (1994)
Habitat of spawning sites; average water depth	Flowing water over gravel or vegetation; sometimes spawns in nests of large centrarchids (Sunfishes)	Carr (1942), Fuiman (1979)
Incubation period; larval type at hatching	4–8 days at 15–29.4°C; yolk-sac larva	Cooper (1935), Carnes (1958)
Mean size at hatching and swim-up	4.4 mm TL, 7–8 mm TL	Carnes (1958), Fuiman (1979)
Parental care	Males defend spawning sites	Page & Johnston (1990)
Major dietary items (adults)	Crustaceans and insect larvae, filamentous algae, copepods, cladocerans, chironomids	Ewers & Boesel (1935)
General year-round habitat	Slow to still waters, including oxbows, sloughs, impoundments, some vegetation present over sand or silt	P. W. Smith (1979), Burr & Warren (1986), Pflieger (1997), Ross (2001)
Migratory or diadromous	Moves to small sloughs or ditches to spawn	Page & Johnston (1990), Boschung & Mayden (2004)
Imperilment status	*E. tenuis* in decline in some localities	Boschung & Mayden (2004)

[1] Given as Practical Salinity Unit.

facilitated by a square arrangement of UV-sensitive double cones in the centrotemporal retina. The double cones of the White Sucker are arranged in a random mosaic rather than in a square pattern, display a substantial size disparity between members of a given cone pair, and are separated more proximally than the double cones of other UV-sensitive fishes. Though sensitive to UV light, the White Sucker is not polarization sensitive. Microspectrophotometer analyses further revealed that the red visual pigments of the White Sucker absorb extremely long wavelengths of ≤630 nm, among the longest wavelength absorption of any vertebrate studied (Flamarique & Harosi 1997; Flamarique & Hawryshyn 1998).

Interestingly, *X. texanus* uses UV visual sensitivity in communication between spawning males. Males defending a spawning territory quickly roll their eyes when another male passes overhead, exposing the portion of the eye that reflects UV light. The UV-sensitive cones of *X. texanus* are located on the dorsal portion of the retina, making them well suited to detect these UV flashes that signal a given spawning territory is occupied (Flamarique et al. 2007).

Hearing

To our knowledge, only a single study has included catostomids in assessing sensitivity of fishes to environmental noise. *Catostomus catostomus*, as well as Lake Chub (*Couesius plumbeus*), exhibited responses to noises ranging from 100 to 1,600 Hz (Mann et al. 2007). This broad range of detection is not surprising given the well-developed Weberian apparatus of cypriniform fishes.

Table 13.8. Life history traits of *Hypentelium*.

Life History Traits	Description	References
Strictly freshwater (ppt)	Yes	
Critical thermal maxima	30.8°C	Kowalski et al. (1978)
Maximum size recorded in length and weight	462 mm; weight not given	Page & Burr (1991)
Maximum age	9–11 years	Raney & Lachner (1946b)
Age and size at first reproduction	1–3 years; 70–170 mm	Carlander (1969), Scott & Crossman (1973), Trautman (1981)
Iteroparous or semelparous	Iteroparous	Kay et al. (1994)
Fecundity estimates (ovarian counts)	About 500–2,700	O'Kelley & Powers (2007)
Mature egg diameter	1.5–2.8 mm	O'Kelley & Powers (2007)
Egg deposition sites	Near head of riffles, other silt-free areas in third-order streams	Curry & Spacie (1984), Jenkins & Burkhead (1994)
Range of nesting dates and temperatures	April–May; 11–17°C	Auer (1982), O'Kelley & Powers (2007)
Habitat of spawning sites; average water depth	Small to medium-sized streams	Adams & Hankinson (1928)
Incubation period; larval type at hatching	10 days at 17.4°C; yolk-sac larva	Buynak & Mohr (1978)
Mean size at hatching and swim-up	9–10 mm	Buynak & Mohr (1978)
Parental care	None	
Major dietary items (adults)	Dipteran larvae, crustaceans, diatoms, detritus	O'Kelley & Powers (2007)
General year-round habitat	Riffles and runs of high-gradient streams and small rivers	Boschung & Mayden (2004)
Migratory or diadromous	Descends to slower, larger streams to spawn	Curry & Spacie (1984)
Imperilment status	Secure	Boschung & Mayden (2004)

BEHAVIOR

Larval Behavior

Laboratory experiments and field observations suggest positive phototaxic (reactive to light) behavior among juvenile catostomids (Hogue & Buchanan 1977). Schooling behavior among swim-up larvae is strongest during daylight hours with individuals dispersing to benthic refugia after sunset (Kennedy & Vinyard 1997). Field surveys document the effectiveness of light traps in estimating larval catostomid densities, further corroborating a photic attraction by these fishes (Mueller et al. 1993; Snyder & Meismer 1997). The intensity of phototaxic response decreases with age and development.

Schooling Behavior and Alarm Signaling

Catostomids retain schooling behavior through maturity, a behavior that is most often observed during spawning migrations (see reproduction section). Brief descriptions of non-reproductive schooling behavior are available for *Erimyzon* (Jenkins & Burkhead 1994), Warner Sucker (*Catostomus warnerensis*, Kennedy & Vinyard 2006), and *Carpiodes* (Trautman 1981). Schooling behavior is intensified when predators threaten the school. Like other ostariophysans, Suckers have evolved a defense system involving alarm pheromones and receptors (see physiology section). The fright reaction, or Shreckreaktion, of Suckers is typical of other ostariophysans, including increased respiratory rate, dashing movements, fin twitching, and increased schooling density (Lawrence & Smith 1989).

Rheotaxis and Thigmotaxis

As Suckers mature, a rheotactic (reactive to current) response determines body and fin position in the water column. Adults and late juveniles of all species are positively rheotactic, generally facing into the current during normal activity. The anal fin is particularly important in maintaining body position, which facilitates spawning in riverine habitats (McCart & Aspinwall 1970).

Table 13.9. Life history traits of *Ictiobus*.

Life History Trait	**Description**	**References**
Strictly freshwater (ppt)	Yes, 6.5[1]	Echelle et al. (1972)
Critical thermal maxima	31.3°C	Lutterschmidt & Hutchison (1997)
Maximum size recorded in length and weight	780 mm; 39.9 kg	NCWRC (2008)
Maximum age	23+ years	Wrenn (1968)
Age and size at first reproduction	3–4 years; 30–48 cm TL	Wrenn (1968), Ross (2001)
Iteroparous or semelparous	Iteroparous	Kay et al. (1994)
Fecundity estimates (ovarian counts)	18,000–800,000	Etnier & Starnes (1993), Ross (2001), Boschung & Mayden (2004)
Mature egg diameter	1.6–2.1 mm fresh, 2.4–2.7 mm hardened	Wrenn (1968), Yeager (1980), Kay et al. (1994)
Egg deposition sites	Inundated shallows, clear streams	Burr & Heidinger (1983), Piller et al. (2003)
Range of nesting dates and temperatures	Early spring to early autumn; 14–27°C	Boshung & Mayden (2004)
Habitat of spawning sites; average water depth	Inundated shallows, clear streams; 0.3–0.5 m	Burr & Heidinger (1983), Piller et al. (2003)
Incubation period; larval type at hatching	1–8 days, 19–24°C; yolk-sac larva	Giudice (1964)
Mean size at hatching and swim-up	4.2–6.8 mm	Yeager & Baker (1982)
Parental care	None	
Major dietary items (adults)	Varies with species; plankton, detritus, algae, bivalves.	McComish (1967), Minckley et al. (1970), Starostka & Applegate (1970), Tafanelli (1970)
General year-round habitat	Main channels of large rivers, reservoirs	Boschung & Mayden (2004)
Migratory or diadromous	Spawning migrations	Burr & Heidinger (1983), Piller et al. (2003)
Imperilment status	*I. labiosus*, Vulnerable	Jelks et al. (2008)

[1] Salinity at collection locality.

Most riverine Suckers are thigmotactic (i.e., respond to hard surface), using their pectoral fins to support the body above the substrate (fin standing, Lundberg & Marsh 1976). Associated with this behavior are morphological adaptations that strengthen the pectoral fins, including simplification of the anterior pectoral fin rays and foreshortening of the fin-ray segments (see morphology section; Lundberg & Marsh 1976). When exposed to intense current, catostomids exhibit pectoral fin appression that increases friction and reduces lift (Fig. 13.21). Both rheotactic and thigmotactic acclimation coincide with the transition to a benthic lifestyle as juveniles (see ecology section).

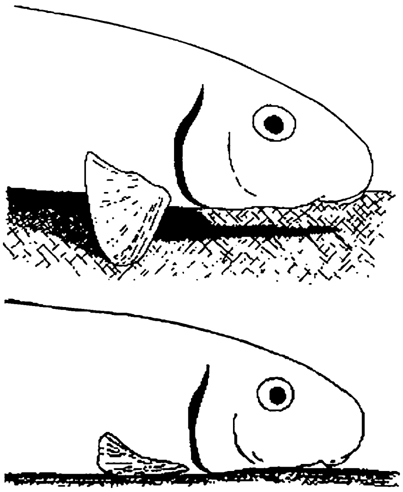


Figure 13.21. Fin standing (*top*) and fin appression (*bottom*) in Silver Redhorse, *Moxostoma anisurum* (modified from Lundberg & Marsh 1976 and used with permission from The American Midland Naturalist, copyright 1976).

REPRODUCTION

Migration and Homing Tendency

Many catostomids migrate annually to and from spawning localities (Breder & Rosen 1966; Curry & Spacie 1984).

Table 13.10. Life history traits of *Minytrema*.

Life History Traits	Description	References
Strictly freshwater (ppt)	Yes	
Critical thermal maxima	>31°C	Reutter & Herdendorf (1976)
Maximum size recorded in length and weight	495 mm TL; weight not given	Lambou (1961)
Maximum age	10+ years	Boschung & Mayden (2004)
Age and size at first reproduction	1–4 years; 150–300 mm	White & Haag (1977), Boschung & Mayden (2004)
Iteroparous or semelparous	Iteroparous	Kay et al. (1994)
Fecundity estimates (ovarian counts)	19,600–51,000	White (1974)
Mature egg diameter	2.3–2.6 mm hardened	Boschung & Mayden (2004)
Egg deposition sites	Riffles and shoals above pools, in depressions behind large rocks	McSwain & Gennings (1972), Hogue & Buchanan (1977), Pflieger (1997)
Range of nesting dates and temperatures	March–May; 12–20°C	Kay et al. (1994)
Habitat of spawning sites; average water depth	Riffles and shoals above pools	Hogue & Buchanan (1977), Pflieger (1997)
Incubation period; larval type at hatching	4.5–12 days, 14–20°C; yolk-sac larva	Hogue & Buchanan (1977), Pflieger (1997)
Mean size at hatching and swim-up	6 mm, 10 mm	Kay et al. (1994)
Parental care	None	
Major dietary items (adults)	Copepods, cladocerans, chironomid larvae	White & Haag (1977)
General year-round habitat	Generalist; streams, rivers, and lakes	Boschung & Mayden (2004)
Migratory or diadromous	No	Kay et al. (1994), Boschung & Mayden (2004)
Imperilment status	Localized population declines	Boschung & Mayden (2004)

These migrations can range from a few hundred meters (e.g., *Hypentelium*, Matheney & Rabeni 1995) to several hundred kilometers (e.g., *Cycleptus*, *Ictiobus*; Fig. 13.18c; Hesse et al. 1982; Mettee 2000; Peterson et al. 2000). Migratory behavior associated with reproduction is documented in *Catostomus* (Olson & Scidmore 1963; Werner 1979; Kennen et al. 1994; McKinney et al. 1999; Douglas & Douglas 2000; Doherty et al. 2010), *Carpiodes* (Madsen 1971; Parker & Franzin 1991; Bonneau & Scarnecchia 2002), *Chasmistes* (Scoppettone et al. 1983; Scoppettone & Vinyard 1991), *Cycleptus*, *Deltistes* (Golden 1969), *Hypentelium*, *Ictiobus* (Bulow et al. 1988), *Minytrema* (McSwain & Gennings 1972), *Moxostoma* (Bulow et al. 1988; Parker & Franzin 1991; Cook & Bunt 1999), and *Xyrauchen* (Tyus 1987; Tyus & Karp 1990). *Cycleptus meridionalis* (Southeastern Blue Sucker) demonstrates a remarkable homing tendency to spawning sites with individuals returning year after year to a single brush pile to spawn (S. Mettee, pers. comm.). Increased water flow due to snowmelt or rain, rather than temperature, is the primary cue triggering spawning migrations in many Suckers (Lucas & Baras 2001; see also spawning season and conditions subsection).

Spawning

One of the earliest notes on spawning in Suckers is by Reighard (1904), who presents a brief account of spawning behavior in *Ictiobus niger* (Fig. 13.18bc). Later, Reighard (1920) provided detailed descriptions of spawning behavior and sexual dimorphism in *Catostomus commersonii*, Pealip Redhorse (*Moxostoma pisolabrum*), and Northern Hog Sucker (*Hypentelium nigricans*). Spawning behavior is surprisingly similar for most species of catostomids, and the following summary of generalized spawning behavior is from Reighard (1920) and Page & Johnston (1990). Suckers generally spawn in the spring over rubble, gravel, or coarse sand substrates (Tables 13.2–13.13; Figs. 13.18d and 13.22); *Erimyzon oblongus* will also spawn over vegetation. Stream- and river-dwelling Suckers spawn in shallow riffles with moderate to fast currents. Lake-

Table 13.11. Life history traits of *Moxostoma*.

Life History Trait	Description	References
Strictly freshwater (ppt)	Yes, 4–6[1]	Walsh et al. (1998)
Critical thermal maxima	35.1–35.4°C	Reash et al. (2000)
Maximum size recorded in length and weight	76 cm TL; 8 kg	RRCC (2010)
Maximum age	8–30+ years	Meyer (1962), Mongeau et al. (1992)
Age and size at first reproduction	2–5 years; size varies	Meyer (1962)
Iteroparous or semelparous	Iteroparous	Kay et al. (1994)
Fecundity estimates (ovarian counts)	1,000–44,000	Jenkins & Burkhead (1994)
Egg diameter (mature ova)	2.6–4.4 mm	Kay et al. (1994)
Egg deposition sites	Shallow riffles or deep runs over gravel	Etnier & Starnes (1993), Jenkins & Burkhead (1994), Boschung & Mayden (2004)
Range of nesting dates and temperatures	9–31°C	Jenkins & Burkhead (1994), Kay et al. (1994)
Habitat of spawning sites; average water depth	Shallow riffles or deep runs over gravel	Etnier & Starnes (1993), Jenkins & Burkhead (1994), Boschung & Mayden (2004)
Incubation period; larval type at hatching	3–9 days at 14.4–22°C; yolk-sac larva	Kay et al. (1994)
Mean size at hatching and swim-up	7.7–11 mm hatching	Kay et al. (1994)
Parental care	None	
Major dietary items (adults)	Varies among species	Trautman (1981), Boschung & Mayden (2004)
General year-round habitat	Small to large rivers; some species adapt to reservoirs	Trautman (1981), Etnier & Starnes (1993), Boschung & Mayden (2004)
Migratory or diadromous	Spawning migrations	Etnier & Starnes (1993), Jenkins & Burkhead (1994), Boschung & Mayden (2004)
Imperilment status	Seven species Vulnerable to Endangered, one species Extinct	Jelks et al. (2008)

[1] 100% juvenile mortality when acclimated in soft water.

dwelling Suckers either migrate upstream to spawn in riffles within tributaries or spawn over coarse substrates along shallow lake shorelines. *Ictiobus cyprinellus* and *I. niger* typically use inundated floodplains (a behavior not observed in *I. bubalus*) but may spawn along shorelines or ascend streams (Fig. 13.18bcd) if floodplains are unavailable (Yeager 1936; Johnson 1963; Trautman 1981). In streams, male Suckers congregate over spawning beds, while females occupy deeper pools upstream of the riffle. When ready to spawn the female drifts tail-first downstream into the spawning area and is approached from either side by >2 males (Fig. 13.18c and Fig. 13.22). Males press against the female, and the fish vibrate rapidly while releasing their gametes. A single spawning act generally lasts <10 s. Males often rub or prod the female with tubercles, which is thought to stimulate egg release. In many species of Suckers, rapid movements that shuffle the substrate during spawning crudely bury the demersal eggs. An interesting exception to this pattern occurs in *I. cyprinellus* in which trios spawn near the water surface, broadcasting eggs over a wide area (Burr & Heidinger 1983). Defense of spawning territories following egg deposition is generally not reported for Suckers, with the exception of *E. oblongus*, which does defend the spawning territory for an unknown duration following spawning (Page & Johnston 1990). To our knowledge, no species of Sucker exhibits active parental care of eggs, larvae, or juveniles.

In many species of Suckers two or more males are involved in a spawning act with a single female (Figs. 13.18c and 13.22). This spawning pattern, known as male simultaneous reproductive parasitism, occurs in many families of fishes (Taborksy 1994). For example, as many as 12 male *H. nigricans* may be involved in a single spawning act (Reighard 1920). *Chasmistes cujus* spawns in clusters of two to seven individuals involving various combinations of males and females (Scoppettone et al. 1983). In contrast, *E. oblongus* most often spawns in pairs, which may

Table 13.12. Life history traits of *Thoburnia*.

Life History Trait	Description	References
Strictly freshwater (ppt)	Yes	Jenkins & Burkhead (1994)
Critical thermal maxima	Unknown	
Maximum size recorded in length and weight	192 mm TL; weight not given	Jenkins & Burkhead (1994)
Maximum age	5–7 years	Raney & Lachner (1946a), Timmons & Ramsey (1983)
Age and size at first reproduction	2–3 years; 94–130 mm TL	Raney & Lachner (1946a, 1946c), Jenkins & Burkhead (1994)
Iteroparous or semelparous	Iteroparous	Jenkins & Burkhead (1994)
Fecundity estimates (ovarian counts)	700–2,000	Raney & Lachner (1946a), Etnier & Starnes (1993)
Mature egg diameter	Unknown	
Egg deposition sites	Buried in gravel, small cobble	Smith (1999)
Range of nesting dates and temperatures	March–May; 12–18°C	Raney & Lachner (1946c), Bailey (1959b), Jenkins & Burkhead (1994)
Habitat of spawning sites; average water depth	Gravel bars, riffles; 8 cm	Bailey (1959b), Smith (1999)
Incubation period; larval type at hatching	Unknown	
Mean size at hatching and swim-up	Unknown	
Parental care	None	
Major dietary items (adults)	Algae, chironomid larvae, detritus	Flemer & Woolcott (1966), Jenkins (1970)
General year-round habitat	Primarily clean gravel, rubble, or boulder sections of streams with strong current	Jenkins & Burkhead (1994)
Migratory or diadromous	No	
Imperilment status	*T. atripinnis* and *T. hamiltoni*, Vulnerable	Jelks et al. (2008)

be associated with their preference for spawning in small headwater streams (Page & Johnston 1990).

As might be expected given the group-spawning behavior of most catostomids, unequal sex ratios often occur in spawning locations where males can greatly outnumber females. A male to female ratio of 1.61M:1F in *Xyrauchen texanus* occurred in spawning reaches of the Green River, Utah (Tyus 1987). In spawning areas of *C. commersonii*, males can outnumber females by ratios of 2.7–2.9M:1F (Fig. 13.22d; Quinn & Ross 1985), but equal numbers of spawning males and females also are observed (Raney & Webster 1942). Of 25 spawning *Moxostoma macrolepidotum* captured, 23 were male (Burr & Morris 1977). Likewise, 77% of Mountain Sucker (*Catostomus platyrhynchus*) captured from a spawning aggregation were male. Unequal sex ratios may simply reflect the fact that males remain at the spawning site while females leave after spawning (Wydoski & Wydoski 2002).

Alternative Spawning Tactics by Males

Male *Moxostoma duquesnei* not actively engaged in a spawning trio were observed positioning themselves upstream of an active spawning trio and rapidly vibrating, presumably releasing milt in an attempt to fertilize the eggs (Bowman 1970). Such behavior might represent an alternative male spawning behavior (i.e., satellite males) that occurs in other families such as Sunfishes and Trouts and Salmons (Taborksy 1994). To our knowledge, no one has examined potential alternative male spawning behaviors in Suckers with appropriate molecular markers for determining paternity.

Spawning Season and Conditions

The length of the spawning season varies greatly in Suckers (Tables 13.2–13.13). Species of *Carpiodes* have comparatively prolonged spawning seasons with Highfin

Table 13.13. Life history traits of *Xyrauchen*.

Life History Trait	Description	References
Strictly freshwater (ppt)	Yes	
Critical thermal maxima	36.7–39.1°C[1]	Carveth et al. (2006)
Maximum size recorded in length and weight	0.9 m TL; weight not given	Sigler & Sigler (1987)
Maximum age	44+ years	McCarthy et al. (1987)
Age and size at first reproduction	Males, 2 years, about 40 cm TL; females, 2–3 years, 40+ cm TL	Sigler & Sigler (1987)
Iteroparous or semelparous	Iteroparous	
Fecundity estimates (ovarian counts)	27,000–144,000	McAda & Wydoski (1983), Minckley (1983)
Mature egg diameter	1.8–2.9 mm	Minckley & Gustafson (1982)
Egg deposition sites	Cobble and gravel substrates	Minckley (1983), Tyus & Karp (1990)
Range of nesting dates and temperatures	April–June; 9–20°C	Bestgen (1987), Tyus (1987), Tyus & Karp (1990)
Habitat of spawning sites; average water depth	Near inflowing rivers or streams over cobble and gravel substrates; 0.25–1.5 m	Tyus & Karp (1990)
Incubation period; larval type at hatching	4–6 days, 20°C; yolk-sac larvae	Sigler & Sigler (1987)
Mean size at hatching and swim-up	6.5–8.6 mm TL; 8.4–8.6 mm TL	Marsh (1985)
Parental care	None	
Major dietary items (adults)	Midge larvae, planktonic crustaceans, diatoms, filamentous algae, and detritus	Marsh (1987)
General year-round habitat	Main-stem medium to large rivers, reservoirs	Moyle (2002)
Migratory or diadromous	Spawning and post-spawning migrations	Tyus (1987), Modde & Irving (1998)
Imperilment status	Endangered	Jelks et al. (2008)

[1] Based on acclimation temperatures of 25 or 30°C.

Carpsucker (*Carpiodes velifer*) and *C. cyprinus* spawning from late June through September (Woodward & Wissing 1976) and River Carpsucker (*Carpiodes carpio*) spawning from early April through August (Jester 1972). Most other catostomids have shorter spawning seasons. The shortest spawning period reported for Suckers is that of *C. cujus*, which may be as brief as 7 days (Scoppettone et al. 1983). Autumn spawning occurs in *Catostomus discobolus* and Flannelmouth Sucker (*Catostomus latipinnis*) and is associated with off-season tributary outflows (Douglas & Douglas 2000).

The time of day during which peak spawning takes place varies among species and even among populations in some species (Fig. 13.22). Spawning frequency is greatest at night for *C.* (Raney & Webster 1942) and *C. cujus* (Scoppettone et al. 1983) with individuals inhabiting deeper water in nearby pools during the day. *Moxostoma macrolepidotum* spawning occurred in direct sunlight during the late morning and early afternoon (Burr & Morris 1977). In contrast, others asserted that spawning in *M. macrolepidotum* may take place in the evening or early morning (Eddy & Surber 1943; Scott & Crossman 1973).

Catostomids spawn over a broad range of water temperatures, but spawning response to water temperature may be species-specific and may have significant effects on both the timing and success of spawning. *Catostomus platyrhynchus* spawn at water temperatures of 9–11°C (Wydoski & Wydoski 2002), but *C. cyprinus* and *C. velifer* may spawn in water as warm as 28°C (Woodward & Wissing 1976). The timing of spawning runs may be influenced by water temperature in some species of catostomids. The peak spawning run of *C. commersonii* began when the water temperature reached about 7°C, but the run was interrupted when the water temperature dropped (Raney & Webster 1942). Little or no recruitment of *X. texanus* occurred when spawning in 10–18°C water in the Green River, Utah, suggesting lowered water temperature from hypolimnetic

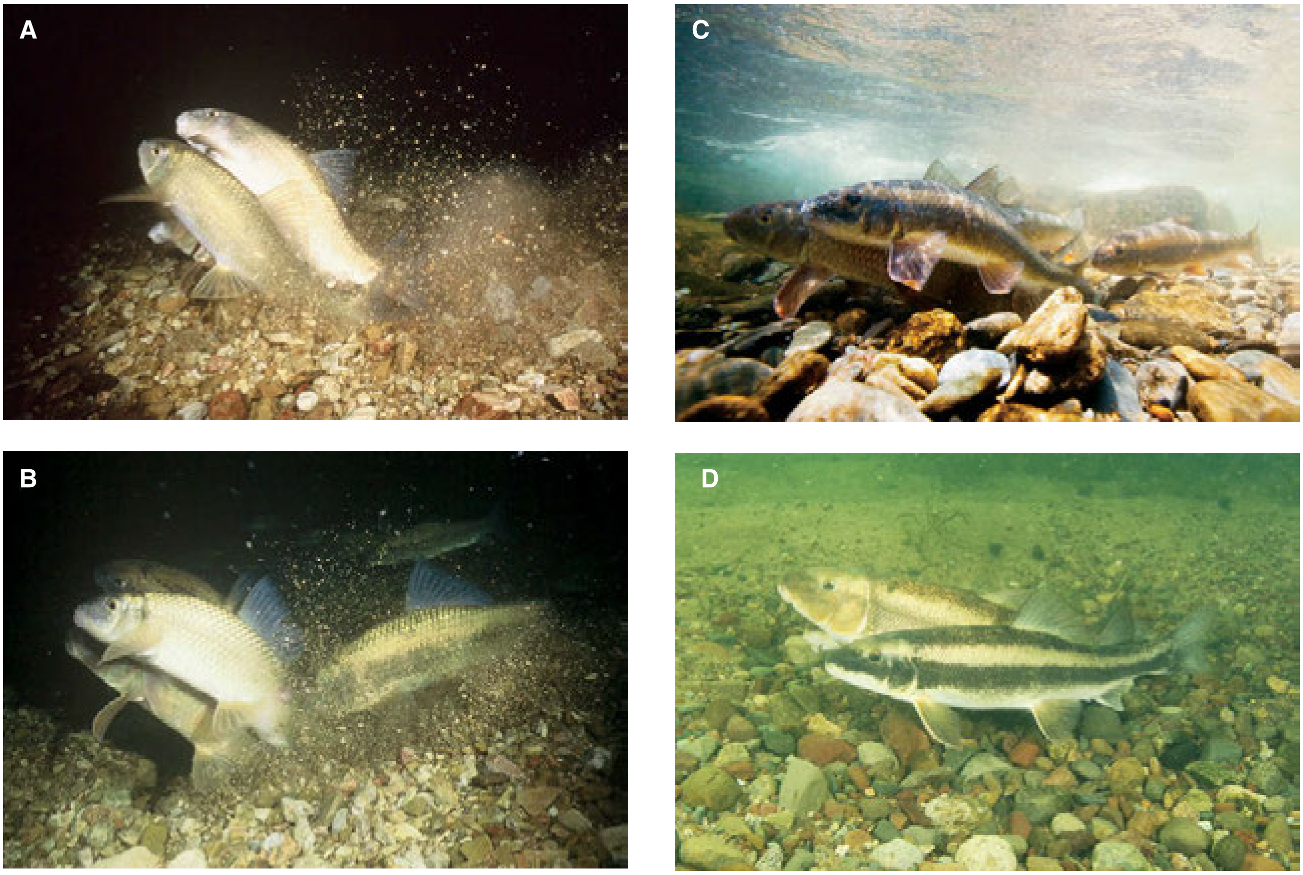


Figure 13.22. Suckers spawn both at night and during the day as exemplified by these groups of Golden Redhorse, *Moxostoma erythrurum* (A–C) and White Suckers, *Catostomus commersoni* (D): (A) at night two Golden Redhorse males quivering in loose gravel with a single female as eggs and milt are released; (B) a similar scene but with a trio of males attempting to mate with a single female (photographed in the Current River, Missouri, from an underwater blind by and used with permission of W. N. Roston); (C) during daylight, two Golden Redhorse males surround a female and a third male lags behind; note the breeding tubercles on the snout of the male in the foreground (photographed in Citico Creek, Monroe County, Tennessee; photograph by and used with permission of Jeremy Monroe, Freshwaters Illustrated); (D) two White Sucker males sandwich a female as they spawn over coarse, clean gravel in Sand Lake, Dresser, Wisconsin in May 2012; note the dark lateral stripe of the spawning male (foreground) (photograph by and used with permission of ©Roger Peterson / Engbretson Underwater Photography).

discharges from Flaming Gorge Dam reduced juvenile recruitment (Tyus 1987). The eggs of *X. texanus* hatch best at 20°C, show significantly lower hatching success at 15°C, and are killed at 5–10°C (Marsh 1985).

Non-annual Spawning

Non-annual spawning is documented in several species of catostomids. In *C. commersonii*, non-annual spawning was correlated with nutritional and physiological stress. Onset of sexual maturity was energy dependent in populations of *C. commersonii* in Gullfeather Lake, Ontario, and was delayed by hypoxic conditions and low densities of chironomid prey (Trippel & Harvey 1989). Individual *C. commersonii* in the Mill River, Massachusetts, also spawned on a non-annual basis. Fish in this population, however, displayed rapid annual growth rates, suggesting that refraining from spawning in a given year is an adaptive strategy to increase future fecundity. Males were three times as likely as females to spawn in a given year, but spawning frequency in females increased with age (Quinn & Ross 1985). Long-lived desert Suckers (e.g., *Chasmistes* and *Deltistes*) can spawn repeatedly over many decades, which compensates for non-annual spawning due to drought

(Coleman et al. 1987; Markle & Cooperman 2001). In the Truckee River, Nevada, *C. cujus* that could not reach the spawning grounds due to drought had higher average fecundities in subsequent years (Scoppettone et al. 2000). Observations of heavy spawning activity of *X. texanus* in 1981, 1984, and 1986, but lack of ripe fish in 1983 and 1985 is also indicative of non-annual spawning in this species (Tyus 1987).

Nest Building, Pit Spawning, and Territoriality

Only one species of catostomid actively constructs nests before spawning. A male *Moxostoma carinatum* constructs a gravel-lined pit 1.2–2.4 m in diameter by sweeping sand and silt away with its caudal fin, sucking up substrate materials with its mouth, and pushing stones with its head (Hackney et al. 1968). Several other species of catostomids spawn over pits, but the pits are either the result of movements of the fish during spawning or are constructed by other species. Abraded caudal and anal fins in spent female Bridgelip Sucker (*Catostomus columbianus*) suggests that they crudely bury their eggs during spawning (Dauble 1986). Burr & Morris (1977) noted that *M. macrolepidotum* spawn over pits. Although they did not observe pit construction, they believed the pits were formed incidental to spawning movements (Fig. 13.22abc). Similarly, disturbance of the substrate during repeated spawning of Golden Redhorse (*Moxostoma erythrurum*, Page & Johnston 1990) and *C. cujus* (Scoppettone et al. 1983) resulted in the formation of pits. Creek Chubsucker (*Erimyzon oblongus*) was observed spawning over pits constructed by Central Stoneroller (*Campostoma anomalum*) or Creek Chub (*Semotilus atromaculatus*, Page & Johnston 1990). Lake Chubsucker (*Erimyzon sucetta*) in Florida laid eggs in the nests of Largemouth Bass (*Micropterus salmoides*, or perhaps, Florida Bass, *Micropterus floridanus*), where the larvae subsequently benefit from the nest-guarding behavior of the male bass (Carr 1942).

Males in *Moxostoma*, *Minytrema*, and *Erimyzon* are territorial during spawning (Page & Johnston 1990). Nevertheless, territoriality may vary among species and even among populations within a given species. Male *Minytrema* guard and defend discrete 3 × 6 m territories by chasing other males for several meters before returning to their territory. Territorial boundaries dissolve only long enough for the formation of spawning trios (Fig. 12.22); competing males attempt to disrupt the trios by swimming rapidly toward them during spawning (McSwain & Gennings 1972). Similarly, *E. oblongus* and *M. erythrurum* establish discrete territories and attempt disruption of spawning trios (Page & Johnston 1990). Male *M. duquesnei* in Missouri defended territories by swimming at intruders with their pectoral fins spread (Bowman 1970). Intruding males quickly retreated, and no physical contact occurred between competing males. The largest males occupied the most upstream territories. In contrast, *M. duquesnei* in Illinois showed no such territoriality during spawning with males frequently changing relative positions. Otherwise non-territorial species within *Moxostoma* may maintain position in spawning aggregations by nudging adjacent males (Page & Johnston 1990) as was observed in Greater Redhorse (*Moxostoma valenciennesi*, Jenkins & Jenkins 1980). Territorial behavior is presumably absent in species of *Cycleptus*, *Ictiobus*, *Carpiodes*, *Catostomus*, and *Hypentelium* (Page & Johnston 1990).

Egg Characteristics and Fecundity

The eggs of catostomids are generally adhesive (Fig. 13.18d) and demersal and range in size from <2 mm in *Carpiodes* to ≤4 mm in some species of *Moxostoma*. Fecundity varies among catostomid taxa with species within Cycleptinae and Ictiobinae displaying higher fecundity than those within Catostominae (Tables 13.2–13.13). Like other fishes, intraspecific fecundity is correlated positively with body size (length or weight; Wagner & Cooper 1963; Woodward & Wissing 1976; Wydoski & Wydoski 2002) but not necessarily with age (Woodward & Wissing 1976; Wydoski & Wydoski 2002).

Species within Cycleptinae and Ictiobinae display remarkably high fecundity. In the Wabash River, Blue Suckers (*C. elongatus*) averaging 668 mm TL and 3.14 kg exhibited a mean fecundity of >150,000 eggs/female with a maximum observed count of 267,471 mature ova (Daugherty et al. 2008; Table 13.5). Female *Ictiobus bubalus* weighing 2.3–2.7 kg produce an average of 230,000 eggs (Wrenn 1968). Fecundity of *I. cyprinellus* is the highest among all Suckers, potentially >800,000 eggs female^{-1} year^{-1} (Kay et al. 1994). In various Iowa lakes, populations averaged about 400,000 eggs female^{-1} year^{-1} (Carlander 1969). *Carpiodes carpio* (288 g, average weight) from the Des Moines River, Iowa, produced between 4,430 and 154,000 ova/female with most females producing <60,000 eggs (Behmer 1969). Fecundity for *C. cyprinus* and *C. velifer* ranged from 15,235 to 63,779 ova and from 41,644 to 62,355 ova, respectively, from females averaging about 200 g (Woodward & Wissing 1976).

Fecundity of fishes within Catostominae is lower than that of Ictiobinae and Cycleptinae. *C. commersonii* is among the most fecund species within the genus with females producing 20,000–50,000 eggs/year (Raney & Webster 1942), followed by *C. latipinnis* (4,000–40,000 eggs; McAda & Wydoski 1983) and *C. occidentalis* (32,300 eggs; Moyle 2002). Smaller-bodied Suckers that inhabit small, swift streams display lower fecundity than larger Suckers. Female Mountain Sucker (*Catostomus platyrhynchus*) may only produce about 2,000 eggs/year (Wydoski & Wydoski 2002). *Hypentelium etowanum* (Alabama Hog Sucker) produces between 493 and 2,717 eggs/female (O'Kelley & Powers 2007) and *Thoburnia rhothoeca* averages <2,000 eggs female^{-1} year^{-1} (Raney & Lachner 1946c). Within *Moxostoma*, *Minytrema*, and *Erimyzon*, fecundity is largely overlapping, ranging from 3,000 to 29,000, depending on body size (140–800 mm) and condition (Meyer 1962; Wagner & Cooper 1963; Hackney et al. 1968; Kay et al. 1994).

ECOLOGY

Habitat Preference and Environmental Tolerance

Catostomids occupy a wide variety of freshwater habitats in North America, from small headwater streams (e.g., some species of *Catostomus*, *Hypentelium*, and *Thoburnia*) to large rivers (e.g., genera *Cycleptus* and *Xyrauchen*) and lakes or reservoirs (e.g., genera *Chasmistes*, *Carpiodes*, and *Ictiobus*). Habitat preferences for some species are difficult to characterize, as preferences change with body and differ geographically. For example, *Minytrema melanops* occurs in small streams and smaller rivers (Ross 2001), reservoirs (Jackson 1957), and oxbow lakes (Beecher et al. 1977). Although environmental tolerances and habitat preferences vary among species, many catostomids are typically associated with well-oxygenated, cool, flowing waters. Most Suckers are relatively intolerant of brackish or stagnant water (see physiology section). Only *Catostomus macrocheilus* and the ictiobines (genera *Carpiodes* and *Ictiobus*) are recorded from brackish bays and inlets (Reimers & Bond 1967). Flow regime, vegetation, substrate type, turbidity, pH, and dissolved carbonates are of varying importance to particular species.

Marked differences in habitat preference are observed between juvenile and adult catostomids. Larval and juvenile forms normally live in open waters near the surface, using terminal mouths to feed on small crustaceans. In many species, larval Suckers seek out shoreline vegetation as shelter (Kay et al. 1994), and juveniles often seek refuge in vegetated backwaters (Barber & Minckley 1966). Juvenile *Chasmistes brevirostris*, *Deltistes luxatus*, and *Catostomus tahoensis* show diel shifts in habitat, migrating to vegetated areas at night and spending daylight hours in open water (Marrin 1983; Simon et al. 2000). Lake-dwelling species of *Erimyzon* are associated with submerged vegetation throughout life, and juveniles almost always occur near dense concentrations of submerged macrophytes (Goodyear et al. 1982; Conrow et al. 1990). Although general patterns of habitat use by larval and juvenile catostomids are often discussed in life history papers, only a few studies have addressed specific habitat use by early life history stages (Kennedy & Vinyard 1997; Markle & Dunsmoor 2007).

Lentic and open-water lotic conditions (i.e., reservoirs) provide habitat and foraging areas for some species of *Carpiodes*, *Chasmistes*, *Erimyzon*, *Ictiobus*, *Minytrema*, and a few species of *Moxostoma*. Large-river habitats are weakly partitioned by sympatric species within both *Ictiobus* and *Carpiodes*. *Ictiobus niger* is more likely to occupy portions of the river with strong currents, but *I. bubalus* prefers areas with fine substrate (Jester 1973; Lee et al. 1981). *Ictiobus cyprinellus*, however, tolerates higher turbidity, lower oxygen concentrations (0.9 ppm), and higher temperatures than congeners (Becker 1983; Pfleiger 1997). In *Carpiodes*, *C. velifer* uses slower water over sand or silt, *C. cyprinus* occupies faster open water, and *C. carpio* occurs in intermediate habitats (Etnier & Starnes 1993; Pfleiger 1997; Boschung & Mayden 2004).

Suckers associated with large river habitats include some species of *Catostomus*, *Cycleptus*, *Carpiodes*, *Ictiobus*, some species of *Moxostoma*, and *Xyrauchen*. Species of *Cycleptus* display possibly the greatest affinity for deeper, faster rivers, favoring areas with swift flow (at least 100 cm/s and ≤260 cm/s) and rarely occur in streams, reservoirs, or backwaters (Rupprecht & Jahn 1980; Moss et al. 1983; Ross 2001). Juvenile *Cycleptus* are described as moving "awkwardly" under slower-flow conditions and irregular substrates (Moss et al. 1983:19).

Small-river habitats are typically inhabited by *Catostomus*, *Hypentelium*, *Minytrema*, and *Moxostoma*. Sympatric species often exhibit fine-scale habitat partitioning in these environments, perhaps to reduce competition, segregating either by substrate, current, or depth, or a combination of these factors. In the Des Moines River, Iowa, co-occurring *Moxostoma macrolepidotum*, *M. erythrurum*, and *M. anisurum* generally occupied different flow regimes (Meyer 1962). *Moxostoma macrolepidotum* occupied the fastest parts of the river, preferring cobble and gravel substrate, but *M. erythrurum* and *M. anisurum* were less particular with regard to substrate, instead choosing habitats with moderate and slow currents, respectively. Bridgelip Suckers (*Catostomus columbianus*) and Largescale Suckers (*C. macrocheilus*) partition river habitat in the North Fork of the John Day River, Oregon, based on depth and current, with *C. macrocheilus* occupying deeper, slower-flowing areas in contrast to *C. columbianus* (Torgersen et al. 2006).

High-velocity streams are favored by the smallest-bodied catostomids. Boulders and cobble promote high insect productivity and provide shelter for fishes that prefer cool, well-oxygenated waters, including small Suckers. As might be expected, headwater species of *Hypentelium*, *Thoburnia*, and small western *Catostomus* are among the least tolerant of siltation and eutrophication (Timmons & Ramsey 1983; Sublette et al. 1990).

Adult Feeding Ecology

Most catostomids are benthic omnivores, but the degree of trophic specialization varies among and within species. Specialists include detritivores, molluskivores, planktivores, and insectivores, but prey preference is flexible and tends toward the most available food item (Welker & Scarnecchia 2003). Feeding habits are typically shared among closely related species, a fact suspected to account for competition between endemic and non-native catostomids in western North America (Pyron 1999). Resource partitioning and character displacement between sympatric catostomids can regulate population and community structure of benthic invertebrates (Dunham et al. 1979; Marrin 1983). Suckers influence community structure by foraging in groups that disturbs microhabitats and allows other fishes access to benthic invertebrates (Jenkins & Burkhead 1994).

Organic material and fish eggs are often reported as part of the diet of Suckers. Algae and detritus are commonly reported items in the diet of adult catostomids, but the relative nutritional importance of such foods is questionable (Ahlgren 1990ab; Jenkins & Burkhead 1994). Detritus was once thought to be a staple food source of most catostomids. Detritus alone, however, does not contain sufficient protein to support growth, but it does provide sufficient energy to supplement protein obtained from invertebrates, and it can provide some sustenance when invertebrates are unavailable (Ahlgren 1990b). Juvenile *Catostomus commersonii* selectively ingest detritus particles that maximize energy and protein content (Ahlgren 1996). Similar to detritus, fish eggs are an uncommon, but well documented, seasonal protein source for some species (Ellis & Roe 1917; Roseman et al. 2009). In fact, many populations of Suckers were once actively reduced by humans based on the assumption that Suckers negatively affect gamefish populations by feeding on eggs (Holey et al. 1979; Holden 1991). This assumption has been refuted, and most fisheries professionals now discourage the unwarranted practice of killing Suckers as “trash fish.”

Feeding habits among species of *Carpiodes* are similar with typical prey items, including detritus, insects, and zooplankton (Walburg & Nelson 1966; Becker 1983). When zooplankton is abundant, however, it may constitute the majority of prey consumed by *C. carpio* (Welker & Scarnecchia 2003).

Species of *Ictiobus* are less detrivorous than those of *Carpiodes*. *Ictiobus bubalus* consumes benthic invertebrates, especially entomostracans and mollusks, when available (Minckley et al. 1970; Vainio 1973). *Ictiobus cyprinellus* is primarily an open-water planktivore, although benthic foods such as insects, mollusks, fish eggs and larvae, and some plant material also are taken (P. W. Smith 1979). *Ictiobus niger* consumes both planktonic and benthic items, depending on resource availability (Minckley et al. 1970; Becker 1983).

The diet of *Cycleptus* consists primarily of invertebrates, especially chironomid, coleopteran, dipteran, trichopteran, and ephemeropteran larvae (Fig. 13.23; Becker 1983; Cowley & Sublette 1987; Peterson et al. 1999). Other items reported in *Cycleptus* diets include hellgrammites (Corydalidae), Fingernail Clams (Sphaeriidae), algae, and leaf litter (Moss et al. 1983).

The lake-dwelling species of *Chasmistes* are adapted for a planktivorous lifestyle. Unlike most Suckers, planktivorous species retain terminal mouths in post-larval life stages, making them well suited to continue to feed on zooplankton in open-water habitats as adults. Although juvenile *C. cujus* and *C. brevirostris* consume zooplankton and chironomid larvae, the diet of adults is primarily zooplankton, although aquatic insects and algae are also reported (Sigler & Sigler 1987; Scoppettone & Vinyard 1991).

Members of *Catostomus* are dietary generalists, but evidence suggests feeding habits are more complex than thought previously (Ahlgren 1996; Saint-Jacques et al. 2000). As adults, all species of *Catostomus* are omnivorous with most preferring soft-bodied invertebrates when available. Gut contents consist primarily of algae, microcrustaceans, or detritus; on average, however, at least 50% of

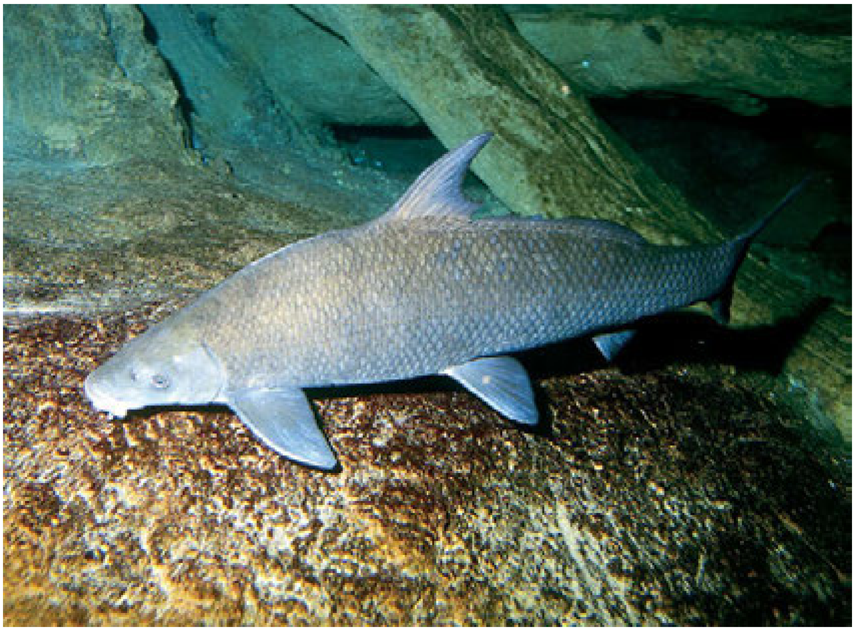


Figure 13.23. Blue Suckers, *Cycleptus elongatus*, forage along bedrock vacuuming up aquatic invertebrate larvae of midges, true flies, caddisflies, and mayflies that inhabit crevices on the rocks' surface (aquarium photograph) (photograph by and used with permission of ©Engbretson Underwater Photographers).

the contents are some type of invertebrate (Stewart 1926; Eder & Carlson 1977; Ahlgren 1990a). Western species of *Catostomus* and *Xyrauchen texanus* primarily consume aufwuchs, a combination of plant and animal material grazed from rocks, although *Xyrauchen* also consumes zooplankton (Clarkson & Minckley 1988; Gregor & Deacon 1988; Sublette et al. 1990). In the Gila River basin, New Mexico and Arizona, *Catostomus clarki* and *C. insignis* partition food resources, *C. clarki* being primarily herbivorous and *C. insignis* consuming high quantities of invertebrates (Smith 1966).

Like *Catostomus*, species of *Erimyzon* and *Minytrema* consume both plants and animals at various stages of their life histories. Cladocerans, copepods, and insect larvae comprise a large proportion of the diets of *Erimyzon* and *Minytrema* throughout all life stages. Adults supplement this diet with the consumption of algae (Ewers & Boesel 1935; White 1974; White & Haag 1977; Sheldon & Meffe 1993).

The genus *Moxostoma* contains some of the most predacious species of Suckers. Seasonally abundant insect larvae are favorite foods, especially caddisflies, mayflies, and midges (Fig. 13.24; Pflieger 1997; Boschung & Mayden 2004). Crayfishes and other crustaceans, fish eggs, and fish fry are occasionally consumed (Jenkins & Burkhead 1994). Most *Moxostoma* also will consume small mollusks, but a few species can take full advantage of this resource. The molluskivores include *M. robustum*, *M. carinatum*, *M. hubbsi*, and *M. valenciennesi*, all of which have robust, molariform pharyngeal teeth used to crush hard-shelled snails, bivalves, and crustaceans (Mongeau et al. 1992; Jenkins & Burkhead 1994). *Moxostoma lacerum* was an extremely specialized molluskivore, apparently extracting the snail body from its shell prior to ingesting the body and operculum and discarding the shell (Jenkins 1994; Fink & Humphries 2010); based on opercula, snails comprised 90% of food items in stomachs (Miller et al. 1989; Jenkins 1994). Early human-induced siltation of eastern rivers, associated with widespread deforestation, would have impaired the ability to sight feed, and *M. lacerum* may have been well on the way to extinction by the mid-1800s (Jenkins 1994). Molluskivorous species of *Moxostoma* may be important in regulating environmental impacts of invasive mollusks, such as the Asian Clam (*Corbicula fluminea*) and Zebra Mussel (*Dreissena polymorpha*). A field experiment showed a 66% reduction in Zebra Mussel biomass, when colonies were exposed to fish predators. Redhorse Suckers were apparently the primary predators; gut contents of 59% of *Moxostoma* individuals contained *Dreissena* shell fragments (Bartsch et al. 2005).

Feeding habits among the three species of *Hypentelium* remain fairly constant throughout all life stages. Insect larvae are the primary prey item from juvenile stages to adulthood (Forbes & Richardson 1909). Relatively small amounts of algae also are taken (Becker 1983). Northern Hog Sucker (*H. nigricans*; Fig. 13.25) is an aggressive feeder that digs prey items from under rocks and debris.

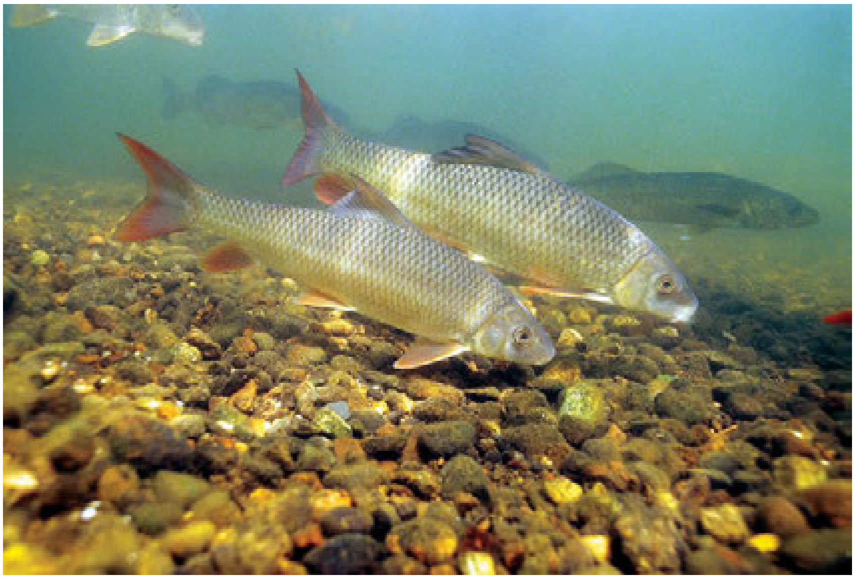


Figure 13.24. Shorthead Redhorse, *Moxostoma macrolepidotum*, shown here foraging along the bottom of the Manitowish River (Vilas County, Wisconsin, September 2007), often feed together in groups with a typical head downward posture, working along the bottom and sucking invertebrates from the gravel (photograph by and used with permission of ©Engbretson Underwater Photography).

Other fishes (e.g., black basses, *Micropterus* spp., and minnows) often follow a Northern Hog Sucker while it forages, feeding on the disturbed invertebrates (Pfleiger 1997). Species of *Thoburnia* consume greater proportions of algae and detritus than *Hypentelium*, although aquatic insects may be taken in high numbers when available (Flemer & Woolcott 1966).

Larval and Juvenile Feeding Ecology

Post–yolk-sac absorption Sucker larvae live in the upper water column, feeding at or near the surface (Yeager 1980; Hogue et al. 1981; Jenkins & Burkhead 1994) on cladocerans, rotifers, copepods, small insect larvae, filamentous algae, and phytoplankton (Stewart 1926; Siefert 1972). Development of larvae into juveniles involves ventral migration of mouthparts, which co-occurs with a transition by juvenile fishes to benthic food sources (Kay et al. 1994; Snyder & Muth 2004). During this period, juveniles feed primarily on cladocerans, copepods, chironomids, and other invertebrates (Adams & Hankinson 1928; Ewers & Boesel 1935; Brown 1984; Markle & Clauson 2009). Interestingly, juvenile Suckers ingest sand or other bottom material, which may provide negative buoyancy necessary for active swimming (Nelson 1959).

Larval ictiobine Suckers begin feeding on zooplankton before absorption of the yolk sac. Juvenile ictiobines depend almost exclusively on cladocerans until shortly after the mouth becomes subterminal (Bucholz 1957; Johnson 1963; Walburg & Nelson 1966; McComish 1967). Other initial foods include copepods, rotifers, algae, and dipteran larvae (Yeager 1980).

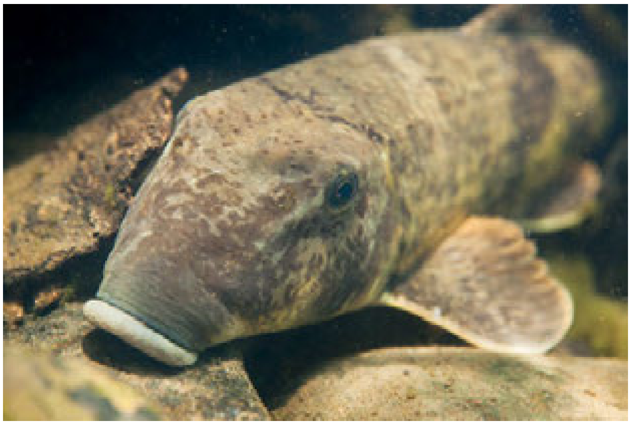


Figure 13.25. A Northern Hog Sucker, *Hypentelium nigricans*, rests on the bottom between aggressive foraging bouts for aquatic insect larvae in the Hiwassee River, Polk County, Tennessee. Note the large, rounded, protrusible mouth and papillose lips (photograph by and used with permission of Jeffrey Basinger, Freshwaters Illustrated).

Age and Growth

Included within Catostomidae are some of the fastest-growing and most long-lived species of North American freshwater fishes (Tables 13.2–13.3). Growth rates are highly variable and are primarily determined by environmental factors. Most species exhibit reduced growth rates at higher latitudes and increased growth rates within preferred habitats. Published lifespan information is inconsistent among studies for many species because techniques of age estimation vary by author (Scott & Crossman 1973). Females generally live longer and grow faster and larger than males but mature more slowly (Scott & Crossman 1973; but see Woodward & Wissing 1976). Reproductive maturity and fecundity are functions influenced more by body size than by age (McComish 1964; Walburg & Nelson 1966).

Ictiobus includes some of the largest and most rapidly growing catostomids, gaining almost 2 mm/week from hatching and reaching 30–70 mm TL within 2 months (Hoyt et al. 1976; Hoyt et al. 1979). Within *Ictiobus*, average lengths at ages 1, 2, and 3 are about 50–180, 130–250, and 300–600 mm TL, respectively (Kay et al. 1994). Rapid early growth among deep-bodied Suckers is suspected to minimize the length of time during which young fish are exposed to heavy predation pressure during the early life history stages in large rivers. Reproductive maturity in *Ictiobus* is attained at 375–480 mm TL and, on average, at about age 4, although fast-growing individuals may mature at age 0, and slow-growing individuals may take 10 years to mature (Walburg & Nelson 1966; Kay et al. 1994). *Ictiobus cyprinellus* matures at a smaller average size (305–375 mm FL) than other *Ictiobus* and may live >26 years (Kay et al. 1994; Paukert & Long 1999).

Growth and maturation in *Carpiodes* is rapid and highly correlated with latitude. *Carpiodes velifer* averages about 65–100, 150–250, and 200–300 mm TL at ages 1, 2, and 3, respectively (Becker 1983; Robison & Buchanan 1988). Growth rates of *C. cyprinus* and *C. carpio* are slightly higher than that of *C. velifer* (Vanicek 1961; Kay et al. 1994). In New Mexico, 25% of male *C. carpio* are mature by age 3, but 25% of females do not mature until age 4 (Morris 1965). Lifespan information with regard to *Carpiodes* is highly variable. Most studies report maximum lifespans of 7–11 years (Morris 1965; Woodward & Wissing 1976). Scale annuli are weakly defined, and age determination is difficult beyond age 5. Some researchers recommend the use of fin-ray cross sections to determine age of specimens >400 mm (Braaten et al. 1999).

Species of *Cycleptus* become reproductively mature at ages 3–11, when individuals are 30–60 cm TL (Kay et al. 1994; Peterson et al. 1999). Maximum age of *C. meridionalis* based on increment analysis of the opercle is 31 for females and 33 for males (Peterson & Nicholson 1997; Peterson et al. 1999). These maximum age estimates probably also apply to *C. elongatus* (Burr & Mayden 1999), but to our knowledge, estimates of the age of this species based on opercular bones are unavailable.

The western North American lake Suckers (genera *Chasmistes* and *Deltistes*) are among the longest-lived catostomids. *Chasmistes cujus* lives ≥40 years, reaching maturity at ages 6–12. In a study of reproductive ecology in *C. cujus*, females at age 44 remained highly fecund and had an estimated reproductive life of 29 years (opercle bone aging; Scoppettone et al. 2000). In the Klamath Basin, California and Oregon, water temperature and dissolved oxygen have substantial effects on growth rates of *D. luxatus* and *C. brevirostris* (Terwilliger et al. 2003). The lifespans of these two species may reach 43 and 33 years, respectively (opercle bone aging; Scoppettone & Vinyard 1991; Markle & Cooperman 2001). *Deltistes luxatus* may attain 91 cm TL; *C. brevirostris* may reach 64 cm TL (Moyle 2002).

Pond-reared *X. texanus* reach maturity at ages 2–6 with males usually reaching maturity more rapidly than females (Minckley et al. 1991). Growth is rapid when food is available and is highest in the population in Lake Mead, Arizona and Nevada (Papoulias & Minckley 1989; Ruppert et al. 1999). A mark-recapture study of the Lake Mead population estimated mean annual growth at 18.7 mm between July and the following June (Ruppert et al. 1999).

Minytrema melanops and *Erimyzon* spp. mature on average at ages 2–4 and 14–30 cm TL (Jackson 1957; Pfleiger 1997). Lifespans of *Erimyzon* spp. and *Minytrema* are 5–6 years and >10 years, respectively (Boschung & Mayden 2004).

Within the redhorse and jumprock Suckers (*Moxostoma*), the Copper Redhorse (*M. hubbsi*) is the largest (>70 cm TL) and most long-lived (>30 years) species. The Blacktip Redhorse (*M. cervinum*) may be the smallest species in the genus with adults averaging 70–165 mm SL (Jenkins & Burkhead 1994); no age estimates appear to be available for this species.

Small, headwater species mature more quickly than large, riverine Suckers. Species of *Hypentelium* and *Thoburnia* mature within 1–3 years at sizes between 7 and 17 cm TL (Raney & Lachner 1946ab; Carlander 1969; Scott & Crossman 1973; Trautman 1981). Though headwater species mature more quickly than larger Suckers such as *Moxoxtoma*, their lifespans are considerably shorter. In New York streams, *H. nigricans* individuals may live ≤10 years (Raney & Lachner 1946b).

Western species of *Catostomus* with limited geographic ranges are generally characterized by short lifespan, small size, and early maturity in comparison to more widespread congeners. In Montana, *C. platyrhynchus* reach means of 93, 116, and 131 mm TL at ages 1, 2, and 3, respectively (Hauser 1969). All individuals matured at ages 3–5.

Minimum size at maturity is 127 mm TL for females and 115 mm TL for males (Hauser 1969; Wydoski & Wydoski 2002). Individuals from a population in Lost Creek Reservoir, Utah, grew faster than those in Montana. Maximum size for *C. platyrhynchus* was 220 mm TL for females and 196 mm TL for males. The oldest observed individuals were age 6 (Wydoski & Wydoski 2002). *Catostomus plebeius* and *C. microps* live <7 years, and mature at age 3+ (Rausch 1963; Moyle & Marciochi 1975; Moyle 1976). Maximum sizes for these species are about 200 mm and 340 mm SL, respectively (Page & Burr 1991). *Catostomus santaanae*, Santa Ana Sucker, is the most short-lived of those few western species for which life history information is available, rarely reaching age 4. Reproductive maturity is attained during the second summer, and maximum size is 160 mm SL (Greenfield et al. 1970). *Catostomus wigginsi*, Opata Sucker, a Mexican endemic, is probably the smallest western Sucker at a maximum size of 127 mm SL (Miller et al. 2005).

Catostomus catostomus, *C. commersonii*, and other widespread Suckers demonstrate length-at-age variation that is not readily attributable to latitude or other regional factors (R. J. Beamish 1973). Growth rates, longevity, and adult body size are extremely variable life history characters within species (Raney & Webster 1942; Chen & Harvey 1999). Lacustrine populations of *C. commersonii* and *C. catostomus* exhibit dwarfism, though sympatric or peripatric populations may attain normal adult body size (Scott & Crossman 1973). Some dwarf populations are designated as subspecies (e.g., *C. catostomus nannomyzon*, and the undescribed Salish Sucker), and others are not (e.g., Jenny Creek Sucker, of *C. rimiculus*), but genetic analyses do not always support such recognition (Dence 1948; Beamish & Crossman 1977). Dwarfism can be regarded as a type of phenotypic plasticity in age and length at maturation and is often associated with habitat differences in productivity or water chemistry or with genetic isolation from other populations (Chen & Harvey 1999). Dwarfism also is reported within populations of *Carpiodes* and *Minytrema* (Trautman 1956; Scott & Crossman 1973).

Competition, Predation, and Non-indigenous Species

Competition among sympatric catostomid species appears to be minimized through character displacement and the partitioning of resources or habitats (Dunham et al. 1979; Marrin 1983; Pyron 1999). In Lake Texoma, e.g., *I. bubalus* consumes greater proportions of copepods than *C. carpio* and is more abundant at greater depth (Gido 2001). Diet overlap occurs among some sympatric species, but Suckers with similar food and habitat requirements are normally peripatric or allopatric (Dauble 1986; Pyron 1999). Little empirical evidence supports strong interspecific competition between Suckers and other native ichthyofauna. Native minnows are most likely to compete with juvenile Suckers in shallow-water habitats. Sturgeons (Acipenseridae) and species of *Moxostoma* may compete for benthic invertebrates in large rivers (Sandilands 1987), and diffuse competition may occur between planktivorous species of *Ictiobus*, shad (Clupeidae), and Paddlefish (*Polyodon spathula*) in the eastern United States (Pfleiger 1997).

Large Asian cyprinids and non-indigenous catostomids are the most direct competitors with native Suckers. Although not yet conclusively demonstrated, the potential for competition exists with several introduced cyprinid species, such as Common Carp (*Cyprinus carpio*), Goldfish (*Carasius auratus*), Black Carp (*Mylopharyngodon piceus*), Bighead Carp (*Hypophthalmichthys nobilis*), Silver Carp (*Hypophthalmichthys molitrix*), Tench (*Tinca tinca*), and possibly Grass Carp (*Ctenopharyngodon idella*; Sanchez 1970; Pfleiger 1997; Fuller et al. 1999; Adámek et al. 2003). This potential negative interaction is inferred from a broad overlap in body size, trophic niche, and habitat preference among native catostomids and invasive Asian cyprinids.

Suckers with restricted distributions seem to be most sensitive to competition with non-indigenous species. In Utah Lake, Utah, indirect competition from introduced Gizzard Shad (*Dorosoma cepedianum*) has negatively impacted the feeding ecology and reproductive biology of the June Sucker (Petersen 1996). Non-native catostomids also can compete with native species for food and optimal habitat, especially during juvenile life stages (Kay et al. 1994), and may negatively impact recruitment of juveniles into the adult population (Padilla 1972).

Introductions of North American freshwater fishes outside of their native ranges may result in the additive detrimental effects of competition and predation on young native Suckers. Widespread introductions of Flathead Catfish (*Pylodictus olivaris*), black basses, crappies (*Pomoxis* spp.), Walleye or Sauger (*Sander* spp.), Temperate Basses (Moronidae), and other piscivores have been detrimental to catostomids west of the western Continental Divide (Lowe et al. 1990; Williams 1995; Fuller et al. 1999). Largemouth Bass (*M. salmoides*) preferentially prey on Desert Sucker (*C. clarkii*) and Sonora Sucker (*Catostomus insignis*) in the Salt River, Arizona (Schwemm & Unmack 2002). Reintroduced *X. texanus* suffer high mortality from predation by non-indigenous ictalurid Catfishes in the Gila River, Arizona (Marsh & Brooks 1989).

Catostomus commersonii is a strong competitor, which may account for its widespread distribution, feasibility in aquaculture, and high abundance in most bodies of water within its range (Saint-Jacques et al. 2000). Introduction of *C. commersonii* outside of its native range influences native community structure, parasite infection rates, geographical distributions, and feeding strategies of native fishes (Hayes et al. 1992; Rodriguez et al. 1993; Dubois 1996; Brodeur et al. 2001). In oligotrophic lakes of Canada, young Brook Trout (*Salvelinus fontinalis*) shifted spatial distribution and feeding habits in the presence of *C. commersonii* (Magnan 1988; Tremblay & Magnan 1991). Similar patterns occurred in studies of interactions between *C. commersonii* and *Perca flavescens* (Yellow Perch). White Suckers grow faster in lakes with piscivores, which may be explained by their superior competitive ability over other species, such as *P. flavescens* (Hayes et al. 1992; Bertolo & Pierre 2005). In Colorado, *C. commersonii* has displaced native Suckers in the Rio Grande and Colorado River drainages (Walker 1993).

Crayfishes are responsible for the most competition with and predation on catostomids aside from the pressures upon catostomids posed by other fishes. Levels of crayfish predation on early life history stages in Suckers can be significant (Mueller et al. 2006). In a density manipulation experiment involving Flannelmouth Sucker (*C. latipinnis*), fish growth was affected to a greater degree by competition with crayfishes than by intraspecific interactions (Carpenter 2005). Polytrophic crayfish species such as *Orconectes virilis* and *Pacifastacus leniusculus* can negatively impact growth and recruitment of western Suckers through competition and predation on juveniles (Lenon et al. 2002; Carpenter 2005). A study of pond-raised *X. texanus* demonstrated intense competition and predation from crayfishes. Lenon et al. (2002) suggested co-culture of Bonytail Chub (*Gila elegans*) as a crayfish predator in order to simultaneously increase productivity in *Xyrauchen* and secure populations of Bonytail Chub.

As an integral part of the food chain catostomids represent an important natural prey item for piscivores in many communities. Lack of fin spines and teeth, high nutritional value, and high abundance contribute to their appeal to apex predators. In northern latitudes, high densities of Suckers represent a valuable food resource for Walleye, Northern Pike (*Esox lucius*), and Muskellunge (*Esox masquinongy*) (Bozek et al. 1999; Chen & Harvey 1999). Suckers are also the primary vertebrate prey item of the River Otter (*Lutra canadensis*) (Berg 1999). Other potential terrestrial predators include pelicans, bears, herons, and fishers (Scoppettone & Vinyard 1991; Hodgens et al. 2004). Species of *Erimyzon* are preyed on by basses (*Micropterus* spp.), pickerels (*Esox* spp.), and Yellow Perch, but *Catostomus* spp. are favored by Walleye, salmonids, and Burbot (*Lota lota*) (Kay et al. 1994). Juvenile *Ictiobus* and *Carpiodes* are seasonally important food items for a range of large-river piscivores. Even so, rapid growth of these deep-bodied Suckers allows individuals to quickly exceed the gape-limitations of many potential predators. Relative pressure from predators strongly influences interpopulational differences in the life history traits of widespread Suckers. In the Canadian Shield, the presence of Northern Pike and Walleye helps to explain differences in the local abundance and longevity of *C. commersonii* (Bertolo & Pierre 2005). Western catostomines are natural prey of pikeminnows (*Ptychocheilus* spp.) and many species of Trouts and Salmons.

Catostomid eggs, being of relatively high abundance during spawning season, are important sources of protein for many fishes, including other Suckers. Eggs of *Ictiobus niger* are consumed by the River Chub (*Nocomis micropogon*), Rock Bass (*Ambloplites rupestris*), Redline Darter (*Etheostoma rufilineatum*), and Greenside Darter (*Etheostoma blennioides*) (Piller et al. 2003). *Moxostoma valenciennesi* eggs are cannibalized by spawning adults and taken by the American Eel (*Anguilla rostrata*), Fallfish (*Semotilus corporalis*), Yellow Perch, and *C. commersonii* in the Thousand Islands region, United States and Canada (Jenkins & Jenkins 1980).

Although a large body of work is published regarding various aspects of catostomid trophic ecology and community structure (e.g., Welker & Scarnecchia 2003; Nelson 2005), a paucity of evidence is available supporting or refuting the idea that Suckers regulate aquatic communities through trophic interactions. This is not too surprising, given that Suckers are opportunistic feeders on a wide variety of food items (Welker & Scarnecchia 2003). Observed variation in local abundance and biomass of Suckers suggest that population dynamics are largely regulated by bottom-up, rather than top-down factors, but this is an area in need of further research (Welker & Scarnecchia 2003).

Productivity, Recruitment, and Drift Ecology

Within a particular body of water, Suckers often occur in extremely high abundance and may account for the greatest per-species biomass. Numerous studies revealed ecological dominance of *C. commersonii* in certain lakes, where populations may account for >50% of the fish biomass (Lalancette 1977; Trippel & Harvey 1987a; Chen & Harvey 1999). Species of *Carpiodes* and *Ictiobus* are consistently among the most abundant fishes sampled in large rivers (Braaten & Guy 1999). Species of *Moxostoma* also occur in high abundance; they comprised >25% of total fish biomass in the Des Moines River, Iowa (Meyer 1962). Other studies reveal species occurring at lower natural densities, such as *Erimyzon oblongus*, averaging 8 adults/ha (Wagner & Cooper 1963).

For most Suckers, especially western species, larval development is intimately associated with flow regime. Young-of-the-year spend the first weeks of life drifting downstream from the spawning area, eventually reaching the basin, lake, or reservoir where they complete development. A few individuals may drift into backwaters or oxbows and return to the main stem after a few weeks. Drift primarily occurs at night, which may reduce the risk of predation. Drift may begin after initial feeding, as inferred from observations of *C. brevirostris* and *D. luxatus* (Cooperman & Markle 2003b). In the Gila River, larval drift samples contained ≤95% catostomids (Bestgen et al. 1987; Sublette et al. 1990). In the Smith and Van Duzen Rivers, California, however, suckers made up a much smaller proportion of larval drift (White & Harvey 2003). Once juveniles are large enough to swim against the current, most move to deeper waters in the lake but may not associate with adult fish (Scoppettone et al. 1983).

Among western Suckers, *Catostomus warnerensis* demonstrates markedly different larval ecology. Young of this species immediately avoid drift by inhabiting refugia in the substrate. In field experiments, larvae resisted downstream transport by using available cover to limit the distance and duration of drift events (Kennedy & Vinyard 1997). This behavior in *C. warnerensis* larvae may have evolved in response to unreliable lake habitat in Warner Valley during the Pleistocene because of climatic fluctuations.

Fish Kills, Diseases, and Die-Offs

Large, highly productive fishes that are not easily caught on hook and line, such as Suckers, have been dubbed “trash fish” by some anglers and, historically, by resource managers. Early efforts to increase sportfish production included widespread use of piscicides (fish poisons) in hopes of reducing competition from Suckers and other putative trash species. The infamous Green River Fish Control Project is among the few deliberate fish kills that received a quantitative evaluation (Binns 1967). Initiated in 1962, this project dumped about 79,500 l of rotenone (a piscicide) into >700 km of the Green River, Wyoming. The combined impacts of rotenone application and the impoundment of Flaming Gorge Reservoir, just downstream, greatly reduced native non-gamefishes, including three species that would later be protected under the U.S. Endangered Species Act. Federal wildlife agencies, urged by nongovernment conservation groups and public media, quickly contested the use of piscicide on native fish populations. Unfortunately, populations of *X. texanus* and numerous cyprinids had already been drastically impacted.

With few exceptions (such as *Ictiobus cyprinellus*), catostomids are relatively sensitive to low oxygen concentrations and pH extremes (Becker 1983). With increasing human disturbance, the frequency of large-scale fish die-offs has increased, especially in isolated western drainages (Perkins et al. 2000). Endorheic lakes in the western United States are subject to large hydrologic fluctuations, which may be natural or anthropogenic in origin. Upper Klamath Lake, Oregon, has experienced dramatic die-offs of *Chasmistes brevirostris* and *Deltistes luxatus.* Large-scale fish kills in upper Klamath Lake and similar watersheds may be attributable to extreme fluctuations in cyanobacteria populations, disease, dissolved oxygen decrease, temperature increase, or any combination of these factors (Scoppettone & Vinyard 1991; Perkins et al. 2000). Man-made reservoirs and developing agriculture synergistically augment these risks by increasing nutrient load and reducing dissolved oxygen levels in the watershed. In Klamath Basin, a disease known as columnaris (caused by *Flavobacterium columnare*) is much more prevalent among Suckers when they are exposed to un-ionized ammonia, low dissolved oxygen, temperature and pH extremes, or combinations of these factors (Marin & Saiki 1999; Markle & Cooperman 2001). Natural die-offs also occur during prolonged drought; however, most native Suckers have evolved behavioral and life history traits that minimize drought mortality. Die-offs also are associated with extreme floods, although these are normally localized events from which catostomid populations quickly recover (Greenfield et al. 1970; Moyle 2002).

Parasitism

Catostomids are hosts to a variety of metazoan ectoparasites and endoparasites, many of which have minimal or unknown impacts on host metabolism and immunological health. In addition to parasite diversity, relative incidence of parasitism in Suckers may exceed that of all other sympatric fishes. In a survey of fish parasites of southeastern Washington, *C. macrocheilus* and *C. columbianus* had the highest rate of infection (91.7%) among all species examined (Griffith 1953). Hoffman (1998) provided a comprehensive list of metazoans known to parasitize catostomids, which includes platyhelminths, nematodes, acanthocephalans, annelids, and arthropods. Catostomid parasites have been characterized primarily in abundant and widespread taxa such as *Catostomus* and *Ictiobus*. The intensity of catostomid parasite infestations often follows a seasonal pattern, as shown in the copepod, *Lernaea cyprinacea*, the trematode, *Triganodistomum attenuatum*, and the cestode, *Glaridacris catostomi* (Whitaker & Schlueter 1975; Muzzall 1980b; Marcogliese 1991).

Parasite diversity and host organ specificity may differ markedly between sympatric Suckers. In Lake Superior, a comparison of parasites in *C. commersonii* and *C. catostomus* found 17 and 8 species, respectively (Hogue et al. 1993). Differences in parasite diversity among sympatric species may be due to host niche breadth (Barton 1980) or temperature limitations as mediated by host habitat preference (Becker 1983). Some catostomid parasites demonstrate strong microhabitat preference that leads to regional specificity within host organs. For example, *Neoechinorhynchus crassus* prefers areas of the gastrointestinal system where aminopeptidase levels are highest (Uglem & Beck 1972). This species occurs in the anterior portion of the gut in *C. macrocheilus* and *C. catostomus*, but prefers the posterior region of the gut in *C. commersonii* (Hogue et al. 1993). Similar patterns are observed in *Triganodistomum attenuatum* (Muzzall 1980a).

Suckers are hosts for freshwater Mussel (Unionoidea) larvae, known as glochidia, that attach to gill or fin membranes. The degree of host specificity for most glochidia-Sucker associations is usually unknown. Some Suckers (as well as other fishes), however, serve as hosts for host generalist mussels (e.g., *Anodonta implicata*, Alewife Floater, *Lampsilis reeveiana brevicula*, Ozark Broken Ray, and *Pyganodon cataracta*, Eastern Floater, host *C. commersonii*, Davenport & Warmuth 1965; OSUMD 2010; *Margaritifera falcata*, Western Pearlshell, host *Catostomus tahoensis*, Murphy 1942). Similarly, the genus *Hypentelium* serves as host to at least four host generalist mussel species (e.g., *Alasmidonta undulata*, Triangle Floater, OSUMD 2010; *L. r. brevicula*, OSUMD 2010; *Lasmigona costata*, Flutedshell, OSUMD 2010; *Strophitus* spp., Haag & Warren 1997; Williams et al. 2008). From a conservation perspective, *H. nigricans* may be one of the most important host species, being the only documented host for the endangered, host specialist Cumberland Elktoe, *Alasmidonta atropurpurea* (Gordon & Layzer 1993).

During freshwater life history stages, Lampreys (Petromyzontidae) can parasitize catostomids, preferring larger species when available. For example, *I. bubalus* are parasitized preferentially by Chestnut Lampreys (*Ichthyomyzon castaneus*) and Ohio Lampreys (*Ichthyomyzon bdellium*) (Metee et al. 1996). Lampreys will, however, attach to catostomids >36 g in the laboratory (Parker & Lennon 1956).

Haff Disease

Haff disease was first diagnosed in patients from the Koenigsberger Haff shore of the Baltic Sea. Discovered in 1924, the disease is characterized by unexplained rhabdomyolysis (muscle cell destruction) following consumption of Burbot (*L. lota*), Eels, or Pikes from Europe, and species of *Ictiobus* from the eastern United States (Centers for Disease Control and Prevention 1998). Once muscle cell membranes are destroyed, cell contents are released into the bloodstream, causing widespread complications.

Signs of Haff disease appear between 30 min and 18 h after consumption, and include severe muscular rigidity, vomiting, and coffee-colored urine. Patients complain of muscle pain, dry mouth, pain to light touch, painful breathing, and whole-body numbness. Laboratory tests reveal elevated levels of creatine kinase and myoglobin in patients' blood (Buchholz et al. 2000). Major symptoms fade after 36 h of treatment, but muscular weakness and soreness may persist for >6 months. Fever is not observed, nor is splenomegaly, hepatomegaly, or neurological anomaly. The etiology of Haff disease is unknown, but in absence of fever the causal agent is deemed a noninfectious toxin (Centers for Disease Control and Prevention 1998). Hexane-soluble, neutral lipids were extracted from leftover fish tissue and, when fed to lab mice, caused red-brown urine and behavioral changes consistent with muscle impairment. Historically, human case fatality is 1% (Zu 1939).

CONSERVATION

Although the 74 species of catostomids in North America represent only about 8% of the species diversity in North American freshwater fishes (Burr & Mayden 1992; Jenkins & Burkhead 1994), about 35% of catostomid taxa are either Endangered, Threatened, or of Special Concern, and three, June Sucker (*C. liorus liorus*), Snake River Sucker (*Chasmistes muriei*), and Harelip Sucker (*M. lacerum*), are extinct (Miller et al. 1989; Warren & Burr 1994; Nelson et al. 2004; Burkhead 2012). Warren & Burr (1994:14) noted that "Suckers . . . are imperiled disproportionately relative to their representation in the total freshwater native fish fauna." At present, eight species and two subspecies are considered endangered in North America based on official conservation status lists: Salish Sucker, *Catostomus catostomus* ssp.; Sonora Sucker, *Catostomus insignis*; Modoc Sucker, *Catostomus microps*; Shortnose Sucker, *Chasmistes brevirostris*; Cui-ui, *Chasmistes cujus*; June Sucker, *Chasmistes liorus mictus*; Lost River Sucker, *Deltistes luxatus*; Lake Chubsucker, *Erimyzon sucetta*; Copper Redhorse, *Moxostoma hubbsi*; and Razorback Sucker, *Xyrauchen texanus* (SEDESOL 1994; USFWS 2010b; COSEWIC 2011). Caveats to the above list are that the Sonora Sucker is known from only two localities in Mexico, hence the inclusion of this species on the SEDESOL list (Miller et al. 2005), and that the Lake Chubsucker is rare in Canada and hence on the Canadian list (COSEWIC 2011). For the Sonora Sucker, both Mexican localities are headwater streams in the Santa Cruz and San Pedro River basins that flow into Arizona, where the species is predominantly found (Minckley 1973). The Lake Chubsucker is not imperiled over its broad range in the United States (Warren et al. 2000; Jelks et al. 2008). Interestingly, eight of these species are from western North America and are restricted in distribution to single drainages or basins with the exception of the Razorback Sucker from the Colorado River basin. Other evaluations by ichthyologists and fisheries biologists of Threatened and Endangered species status based on best available information, however, indicate that an additional 35 taxa are imperiled in part, or all, of their distributions (Table 13.14). Surprisingly, only six species (*Catostomus warnerensis*, *C. liorus*, *D. luxatus*, *Moxostoma congestum*, *Myxocyprinus asiaticus*, and *X. texanus*) are featured in the *Threatened Fishes of the World* series published in *Environmental Biology of Fishes* (Williams 1995; Marsh 1996; Whitney & Belk 2000; Gao et al. 2008; Bean et al. 2009; Evans et al. 2009).

Threats to Suckers (like those affecting other North American freshwater fishes) include dams, diverting water for agricultural purposes, pollution, habitat degradation, introduced species, and a negative image by some fishery managers and the public regarding ecological roles and interactions of Suckers with more "desirable" fishes (Holey et al. 1979; Minckley & Douglas 1991; Minckley et al. 1991; Warren & Burr 1994; Warren et al. 2000; Cooke et al. 2005). Cooke et al. (2005) reviewed the general conservation status of catostomids and presented several regional case studies highlighting threats to these species. Interestingly, they concluded that imperiled Suckers are often faced with multiple threats throughout their life history that have a synergistic effect, magnifying the susceptibility of these species to continuing, long-term threats.

Suckers from the Klamath Basin of southern Oregon and northern California are an excellent example of synergistic effects from multiple threats (see also ecology section). Four species of Suckers inhabit this basin; two species, Shortnose Sucker and Lost River Sucker, occur primarily in upper Klamath Lake, but spawn in tributary streams and rivers or in springs or other areas along the shore of the lake. Both species are long-lived, obligate lake dwellers; sexual maturity occurs between 4 and 9 years of age (Cooperman & Markle 2003a). Historically, large spawning migrations of both species occurred in the Sprague River; these migrations were large enough to support both indigenous and commercial fisheries (Cope 1879; Gilbert 1898). Sport fisheries for both species occurred until their listing as endangered under the U.S. Endangered Species Act (Moyle 2002). In 1914, construction of a dam on the Sprague River effectively blocked access to about 90% of spawning habitat (Cooke et al. 2005). Subsequent development of a federal irrigation project in the basin led to fluctuating lake levels that isolated or dried lakeshore spawning habitats and larval and juvenile Sucker nursery grounds (Markle & Dunsmoor 2007). In addition, larval and juvenile Suckers can be entrained in the primary irrigation canal for this project, carrying them away from the lake. Eutrophication of the lake from increasing anthropogenic activities has negatively affected water quality; pH levels >10.0 and dissolved oxygen concentrations <2.0 mg/l occur (Martin & Saiki 1999). Introduced Fathead Minnow (*Pimephales promelas*) are now the predominant fish in upper Klamath Lake (Simon & Markle 1997) and are a major predator on larval Suckers as they drift from spawning grounds into the lake (Markle & Dunsmoor 2007). Given the complexity of threats facing these two species, and the relatively short period in which this system has been under study, it is not surprising that little scientific consensus exists regarding restoration strategies (Cooperman & Markle 2003a; Cooke et al. 2005). Unfortunately, but not surprisingly, politics

Table 13.14. Conservation status of Suckers (Catostomidae) as recognized by the U.S. Fish and Wildlife Service (USFWS 2011), the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2010), SEDESOL (1994, Mexico), the International Union for Conservation of Nature and Natural Resources Red List (IUCN 2010), and the American Fisheries Society (Jelks et al. 2008). Common and scientific names and conservation status categories follow the designations given by these sources. Status of taxa in Jelks et al. (2008) may be limited to specific ecoregions as listed in their Appendix 1. Conservation status categories are Critically Endangered (CR), Endangered (E), Threatened (T), Vulnerable (V), Rare (R), Special Concern (SC), and Extinct (X).

Common Name	Scientific Name	USFWS	COSEWIC	SEDESOL	IUCN	Jelks et al.
Yaqui Sucker[1]	*Catostomus bernardini*			R	V	V
Cahita Sucker	*C. cahita*			T	V	T
Jasper Longnose Sucker	*C. catostomus lacustris*					T
Salish Sucker	*C.* sp. cf. *catostomus*		E			E
Desert Sucker	*C. clarki*					V
White River Desert Sucker	*C. clarki intermedius*					E
Virgin River Desert Sucker	*C. clarki utahensis*					T
Zuni Bluehead Sucker	*C. discobolus yarrowi*					E
Sonora Sucker	*C. insignis*			E		V
Little Colorado River Sucker	*C.* sp. cf. *latipinnis*					V
Fleshylip Sucker	*C. leopoldi*			R	V	T
Modoc Sucker	*C. microps*	E			E	E
Nazas Sucker	*C. nebuliferus*					T
Goose Lake Sucker	*C. occidentalis lacusanserinus*					V
Rio Grande Sucker	*C. plebuis*					V
Jenny Creek Sucker	*C. rimiculus* ssp.					V
Santa Ana Sucker	*C. santaanae*	T			V	T
Klamath Largescale Sucker	*C. snyderi*				SC	T
Summer Sucker	*C. utawana*					T
Warner Sucker	*C. warnerensis*	T			V	E
Opata Sucker	*C. wigginsi*			T	V	T
Wall Canyon Sucker	*Catostomus* sp.					E
Shortnose Sucker	*Chasmistes brevirostris*	E			E	E
Cui-ui	*C. cujus*	E			CR	E
June Sucker[2]	*C. liorus mictus*	E				E
Snake River Sucker	*C. muriei*				X	X
Blue Sucker	*Cycleptus elongatus*			R	SC	V
Rio Grande Blue Sucker	*Cycleptus* sp. cf. *elongatus*					T
Southeastern Blue Sucker	*C. meridionalis*					V
Lost River Sucker	*Deltistes luxatus*	E			E	E
Lake Chubsucker	*Erimyzon sucetta*		E			
Bigmouth Buffalo	*Ictiobus cyprinellus*		SC			
Fleshylip Buffalo	*I. labiosus*					V
Spotted Sucker	*Minytrema melanops*		SC			
Mexican Redhorse	*Moxostoma austrinum*					V
River Redhorse	*M. carinatum*		SC			
Gray Redhorse	*M. congestum*					T
Black Redhorse	*M. duquesnei*		T			
Carolina Redhorse	*M.* sp. cf. *erythrurum*					E
Copper Redhorse	*M. hubbsi*		E		V	E
Harelip Sucker	*M. lacerum*				X	X

Table 13.14, continued

Common Name	Scientific Name	USFWS	COSEWIC	SEDESOL	IUCN	Jelks et al.
Sicklefin Redhorse	*M.* sp. cf. *macrolepidotum*					T
Robust Redhorse[3]	*M. robustum*					E
Greater Redhorse	*M. valenciennesi*					V
Blackfin Sucker	*Thoburnia atripinnis*					V
Rustyside Sucker	*T. hamiltoni*				SC	V
Razorback Sucker	*Xyrauchen texanus*	E		E	E	E

[1] Miller et al. (2005:145) synonomized *C. conchos* with *C. bernardini* based on meristic counts, morphology, and cranial osteology. Williams et al. (1989) considered *C. conchos* as Special Concern; IUCN (2009) considers both taxa as Vulnerable.

[2] In their revision of *Chasmistes*, Miller & Smith (1981) considered the original June Sucker (*C. liorus liorus*) extinct and described a new subspecies, *C. liorus mictus*, which originated through hybridization between *C. liorus liorus* and Utah Sucker (*C. ardens*).

[3] Williams et al. (1989) cited this taxa as the Bighead Redhorse, *Moxostoma* sp. *Moxostoma robustum* was transferred to the rediscovered Robust Redhorse by Jenkins & Burkhead (1993:491, footnote) and Gilbert (1998).

entered into the debate given the value of agricultural lands irrigated with water from upper Klamath Lake (Cooperman & Markle 2003a). We recommend Cooperman and Markle (2003), and references therein, for a review of the influence of politics on science and restoration efforts for Suckers of Klamath Lake.

Many factors collectively impede conservation efforts for Suckers (summarized by Cooke et al. 2005). Two of these issues we expound on briefly, using catostomids as examples, because of their general relevance to resource management and conservation biology. The first issue is simple identification (taxonomy). Identification of adult Suckers can be somewhat problematic, often requiring a combination of morphological characters to separate closely related species (Etnier & Starnes 1993; Jenkins & Burkhead 1994; Boschung & Mayden 2004); larval and juvenile Sucker identification can be characterized as challenging at best (Fuiman 1979; Fuiman & Witman 1979; Fuiman 1982). The reduction or elimination of organismal courses at many universities over the last two decades has contributed to the decline in taxonomic abilities, or even interest, often seen in today's students, resource managers, and conservation biologists (Noss 1996). The result of this decline is that species that are difficult to identify (e.g., Suckers and minnows) are often pooled with other species in ecological or fisheries studies (Cooke et al. 2005), limiting the value of much of the data in these studies. Concomitant with the decline in taxonomic abilities is a second issue, the decline in life history studies, a paucity that, unfortunately, seems to be rectified only when species are listed as Threatened or Endangered (Simon & Markle 1997; Simon et al. 2000; Cooperman & Markle 2003a; Marsh et al. 2003; Pearson & Healey 2003; Markle & Dunsmoor 2007).

COMMERCIAL IMPORTANCE

Suckers are often characterized by anglers as rough or trash fish because they do not often take a hook and so are not considered sportfishes. The flesh of Suckers is, by many accounts, palatable and sweet but is interspersed with numerous small, Y-shaped intramuscular bones that are difficult to remove and, according to Jordan & Evermann (1902:36), "are very troublesome to one who attempts to eat [a Sucker]." The annoyance of these small bones can be partially ameliorated by scoring the fillet with a sharp knife (Tomelleri & Eberle 1990) or by grinding the flesh in a food processor for use in fried fish cakes. Despite the limitations of catostomids as sport or food fishes, the abundance and large size of Suckers make them a potentially commercially important though underused resource. Several species of Sucker have historically represented an important food source for several tribes of Native Americans. Aquaculture of Suckers, both for human consumption and for use as baitfish, is practiced in North America and in several countries formerly in the Soviet Union (Welcomme 1988). Catostomids have also been used as environmental sentinels in the assessment of the ecological impacts of contamination on affected fisheries.

Human Food

Suckers have historically represented an important source of food for many groups of Native Americans across the continent. *Deltistes luxatus* has long been an important food source for members of the Klamath tribe of Oregon where it has been caught in great numbers during the spring run and cured for consumption throughout the year (Jordan & Evermann 1902). The bones of many species of Suckers are commonly found in Native American middens throughout North America (Etnier & Starnes 1993; Butler 1996, 2001). The mass harvest of Suckers by Native Americans during spring migration runs was facilitated by the construction of funnel-shaped rock piles in streams and shallow river runs (Etnier & Starnes 1993). In addition, early settlers made extensive use of Suckers in their diets in a variety of forms, including fresh, canned, smoked, and salted (Sigler & Sigler 1987).

Harvest of wild Suckers during spring spawning runs continued after European settlement. Suckers in shallow streams or rivers may be speared or snagged with treble hooks (Etnier & Starnes 1993). In the Cahaba River, Alabama, *Moxostoma carinatum* are snared with a slipknot loop attached to a pole by anglers standing on stepladders (Hackney et al. 1968); in deeper waters, migrating Suckers are often trapped or caught in gillnets (Mettee et al. 1996). The large numbers of Suckers harvested in the spring were often salted for use throughout the year (Tomelleri & Eberle 1990).

By far the most commercially important food fishes within Catostomidae are the buffalofishes (*Ictiobus* spp.). In aquaculture, buffalofishes are generally grown in rotation with rice crops in fertilized ponds or in polyculture with Channel Catfish, *Ictalurus punctatus* (McGeachin 1993). *Ictiobus cyprinellus* is the species most often cultured because of its rapid growth, early maturation, and high fecundity (McGeachin 1993). Yields of Bigmouth Buffalo from extensive fertilized rice ponds can reach >1,100 kg/ha and average about 560 kg/ha (Borgstrom 1978). When raised in monoculture, buffalofish stocks are often less expensive to raise than other commercially important fishes because they can be successfully grown without the addition of supplemental feed; when raised in polyculture with Channel Catfish, buffalofishes feed on excess Catfish feed and naturally occurring zooplankton (McGeachin 1993). Buffalofishes reach marketable size from 1–3 kg (McGeachin 1993). The harvest of buffalofishes peaked in 1982 with >14,500 mt captured but declined dramatically in the late 1980s to about 1,800 mt/year harvested from the 1990s to 2004 (FAO 2006).

Baitfish

Because small Suckers are an important natural source of forage for large predatory fishes (Robison & Buchanan 1988), anglers prize them as excellent baitfish. Several species of Suckers are raised in intense aquaculture facilities in North America for use as baitfish. In areas with coldwater fisheries *Catostomus commersonii* are successfully cultured as baitfish (Bandeen & Leatherland 1997). White Sucker fry also are raised for use as feed for cultured esocids such as Northern Pike, *E. lucius*, and Muskellunge, *E. masquinongy* (Westers & Stickney 1993). Chubsuckers (*Erimyzon* spp.) are locally important baitfish to anglers in several warm-water regions (Davis 1993). Both White Suckers and chubsuckers are most commonly intensively cultured in fertilized, earthen ponds without the addition of exogenous feed (Davis 1993). Nevertheless, aquaculturists have had difficulty in growing juvenile White Suckers >1 g of body weight, possibly because of nutritional deficiencies in the natural diets available to juvenile Suckers in ponds under dense stocking conditions (Bandeen 1995). Providing juvenile White Suckers with an exogenous feed originally formulated for salmonids that is high in lipids and protein and low in carbohydrates improved their growth rates (Bandeen & Leatherland 1997).

Ecological Indicators

In addition to the direct use of Suckers as human food or baitfish, Sucker populations may be of considerable economic importance as ecological indicators of the health of ecosystems impacted by low-level contamination. Populations of indigenous, widely distributed fish species with known life history characteristics that are suitable for laboratory research may provide valuable information about ecosystem-level effects of low-level contamination by serving as environmental sentinels (Munkittrick & Dixon 1989). Suckers are particularly well suited to study as ecological indicators of low-level contamination for several reasons. As benthic foragers, Suckers are exposed directly to contaminated sediments, reducing lag time between a contamination event and the detection of its ecological effects (Munkittrick & Dixon 1989). Many species of Sucker mature quickly and are common and easily collected, facilitating the study of relatively short-term population changes. As a consequence, Suckers are ideal indicator species for monitoring environmental quality.

LITERATURE GUIDE

Although a comprehensive book has never been dedicated to the Catostomidae, many of the regional faunal guides provide a wealth of information on the biology, distribution, local importance, and evolutionary relationships of Suckers. Three books, in particular, provide exceptional information and illustrations of eastern North American Suckers: *Freshwater Fishes of Virginia* (Jenkins & Burkhead 1994), *The Fishes of Tennessee* (Etnier & Starnes 1993), and *Fishes of Alabama* (Boschung & Mayden 2004). For western Suckers, we recommend *Inland Fishes of California* (Moyle 2002), *The Fishes of New Mexico* (Sublette et al. 1990), and *Freshwater Fishes of Mexico* (Miller et al. 2005). The field guide by Page & Burr (1991, revised 2011) provides useful information on identification, distribution, and habitat for species of Suckers north of Mexico. Bruner (1991b) compiled a bibliography for the family. Smith's (1992) chapter on the phylogeny and biogeography of catostomids, which is frequently cited in this chapter, provides an excellent review of the historical literature associated with the taxonomy and systematics of the family.

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